COMPATIBILITY AND GENETIC STUDIES

OF SOME *CARICA* SPECIES

AND THEIR HYBRIDS

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ABSTRACT

Experiments were conducted to study floral biology, cross compatibility, heterosis, cytogenetics and inheritance of several morphological characteristics among nine Carica species: Carica cauliflora, C. goudotiana, C. monoica, C. parviflora, C. pennata, C. pubescens, C. papaya, C. horovitziana and Index number 203.

All species studied except C. parviflora showed maximum anthesis between 4 and 10 p.m. C. parviflora showed maximum anthesis between 8 to 10 a.m. The hybrid, C. parviflora (8 - 10 a.m. anthesis time) x C. goudotiana (4 - 6 p.m.) showed maximum anthesis between 10 to 12 noon.

Pollen was successfully germinated at six pH levels ranging from 4.5 - 9.5. A gradual rise in percentage germination of pollen from pH 4.5 - pH 7.5 followed by a sharp drop at pH 8.5 and pH 9.5 was observed in all the species. Results also showed significant differences between species. Pollen of C. goudotiana and C. papaya showed lower germination percentages than pollen of other species.

All species were self compatible. Cross compatibility studies showed crosses that were fertile, crosses which set fruit but produced empty seeds, crosses that set parthenocarpic fruits and crosses that failed to set fruit. C. papaya was cross incompatible with all species used in this study. A new hybrid C. parviflora x C. goudotiana was produced.

A description of ten hybrids developed in this work was presented. All hybrids were fertile. Heterosis for vegetative growth and productivity was conclusively shown in two crosses. Comparisons were

made between the means of hybrids and those of their high parents.

Stem color and petiole color were each shown to be under the control of a single gene pair, red being dominant to green in both cases. Variations in the intensity of red color in stems and petioles were attributed to the possible influence of modifier genes. Monogenic control was established for flower color with purple-blush and white, both dominant to pale yellow flower color. Red ripe skin color of the fruit was dominant to yellow. A cross between plants of red fruit color with those of orange fruit color produced F_1 hybrids with pink colored fruits, indicating lack of dominance between red and orange.

Fruit ridges were dominant to wide grooves which in turn were dominant to narrow grooves. Mode of inheritance was monogenic in both cases. Spiny and non-spiny seed coats were simply inherited with dominance lacking. A single-gene difference between succulent fruit pulp and dry pulp with recessiveness for the latter was shown. A dominant monogenic control of profuse branching over sparse branching was observed.

Crosses between dioecious and monoecious species using pollen from the latter produced only monoecious F_1 plants. The reciprocal cross produced F_1 plants in an approximate ratio of 1 male : 1 monoecious. Differential suppression of androecium observed in crosses between C. monoica and C. goudotiana requires further investigation.

Cytological observations confirmed nine pairs of chromosomes for all species and hybrids investigated. Occasional partial pairing and subsequent precocious anaphasic separation involving one pair of

homologues were observed in all species and hybrids studied. Heteromorphism between these two homologues was detected in three species and three hybrids. These findings seem to support the hypothesis that sex chromosomes do exist in these species and hybrids. Chromosome lagging sometimes observed at anaphase I in two of the hybrids was a new phenomenon in the genus. This feature could result in the evolution of aneuploids in the genus.

High fertility of hybrids was attributed to regularity of bivalent formation. This is suggestive of close genetic affinity between the parent species. Speculations into the potentials of the wild Carica species were discussed.

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INTRODUCTION

By far the best known species of Carica is Carica papaya L., a popular fruit in many tropical areas. The exact number of Carica species is not certain, but a recent taxonomic survey of the family Caricaceae by V. M. Badillo (1967) proposed twenty-one species of Carica. All are native to tropical and sub-tropical America. With the exception of C. papaya most of the species produce small non-edible fruits of little commercial importance.

Attempts to improve the papaya as an economic crop have mostly been limited to intercrossing cultivars within the species. Sometimes desirable strains of the same cultivar have been intercrossed for this purpose. Studies of other species and interspecific hybrids may show the presence of desirable attributes of economic value and produce fundamental knowledge of species relationships.

Some of these species, including C. cauliflora, C. pubescens, C. stipulata and C. candicans have been shown by Horovitz and Jimenez (1967) to be resistant to "distortion ringspot virus" to which the commercial papaya is susceptible. For this reason wild species of Carica are receiving attention from plant breeders as possible sources of genes for climatic adaptation and/or disease resistance.

Unlike C. papaya some of the wild species have very colorful stems, leaf petioles, flowers and fruits. An understanding of mode of inheritance of these traits could lead to their utilization as marker genes. In fact the attractive, colorful appearance of these wild species gives them a potential ornamental value.

Furthermore, the wild species of Carica are not entirely useless as items of food. Horovitz and Jimenez (1967) suggested that some of these species and their virus resistant hybrids offer good possibilities for papaine production. Although many of the Carica species produce small non-edible fruits, some of them do produce edible parts. When Swingle (1947) wrote about the "Peruvian Cooking Papaya" he was referring to C. monoica. The leaves and fruits of this species are eaten by the Peruvians. Two other species, C. goudotiana and C. pubescens are also used as food items (Hamilton, personal communication).

This work is an attempt to study the biology and genetics of some Carica species and their hybrids in order to attain further knowledge of this genus. Information derived from this study could contribute to the improvement of C. papaya as a commercial crop.

LITERATURE REVIEW

INHERITANCE OF COLOR

Inheritance of Flower Color: The only case in which flower color inheritance has been reported in the genus Carica was in C. papaya. In this species Hofmyer (1938) found yellow flower color dominant to white flower color. In the 'Kapoho Solo' purple tinged color is a sex-linked character limited to hermaphrodites. Female flowers are white, (Nakasone, unpublished data).

Elsewhere in the plant kingdom, numerous studies have been done on the mode of inheritance of flower color. In the zigzag plant, Asystasia gangetica, Kamemoto and Storey (1955) found basic flower color to be governed by three independently inherited gene pairs: P, producing purple pigment in the inner epidermis of limb; B, producing purple in the outer epidermis of limb and back of tube; and Y, producing yellow in the entire limb. White flowers result when all three are present as homozygous recessives. Bronze was shown to result from complementary gene action. A cross between purple and yellow produced bronze progenies in the F_1. F_2 progenies segregated in a ratio of 9 bronze : 3 purple : 3 yellow : 1 white.

In the genus Capsicum, Odland (1960) showed purple color of the petal to be dominant to white. The segregation ratios observed in the F_2 and backcross progenies indicated a single gene difference between the parent varieties with respect to petal color. He also found purple anther color dominant to yellow. The mode of inheritance was monogenic.

Desmodium sandwicense had two major flower colors, purple and near-white. Park and Rotar (1968) found this character monogenic with purple dominant to white. These workers also observed a range of variation in color within the colored and white flowered groups. An attempt was made to relate color variability of F_2 progenies to parental color groups but no definite pattern of inheritance was evident.

The general assumption associating dominance with presence of color and recessiveness with absence of color is not always true. Mehlquist (1939) investigated the inheritance of flower color in the carnation, Dianthus caryophyllus. He found red dominant to white, but white was dominant to both yellow and cream. He identified six independent factors concerned with flower color in carnation, Dianthus caryophyllus. Donald W. Davis et al. (1958) also found pink flower color of Impatiens balsamina L. dominant to white but white was dominant to cream. Brewbaker (1962) showed the cyanidin-red color of the corolla in the white clover, Trifolium repens L., a duplicate recessive mutant to white. F_1 progenies in crosses between cyanidin-red and white were white. F_2 progenies segregated in a ratio of 15 white to 1 cyanidin-red. Backcrosses segregated in a ratio of 3 white : 1 cyanidin-red. Brewbaker also found white dominant to pink corolla color.

Paris and Haney (1958) identified 9 genes for flower color in Petunia. Their results indicated very complex interactions of these genes. Cases of the heterozygous condition having a diluting effect have also been reported in Dahlias by Lawrence (1931), in Nicotiana by Smith (1937) and in Asystasia gangetica by Kamemoto and Storey

(1955). Barnes et al. (1960) discovered four different genes controlling flower color in flax. Two of these were pleiotropic, affecting both seed color and flower color.

From the preceding review it appears there is considerable variation in mode of inheritance of flower color in the plant kingdom. In a biochemical survey of factors determining flower color, Scott-Moncrief (1936) stated, "... many different factorial types are involved in flower color variation. In some cases their action is quite independent and their combined effects are purely additive, but in others their interrelationship is expressed by interaction phenomena ..."

Inheritance of Stem Color: The mode of inheritance of purple stem color in C. papaya was reported by Hofmyer (1938). He found purple stem color dominant to green stem color. However, occurrence of different degrees of purple within the purple group was not investigated.

Studies of stem color inheritance in jute, Corchorus capsularis by Gupta and Sarma (1953) revealed variations in color intensity observed within any particular pigmentation group as resulting from combinations of specific alleles in a multiple allelomorphic series controlling pigment distribution and intensity. They classified the eight pigmentation types in Corchorus capsularis into three groups: full green, green-pigmented and red. They postulated three loci involved in the production of these colors. Within each pigmentation group, there is always a single gene difference. Between members of

green-pigmented and red groups, the difference may be monogenic or digenic. Differences between members of the full green and either of the pigmented groups may be monogenic, digenic or trigenic. They found the relationship between dark red and full green to be under the control of two pairs of genes with partial dominance of dark red to full green. Erickson (1963) reported that in a cross between two varieties of Okra, Hibiscus esculentus, one with a solid red stem and petiole and the other with a solid green stem, the F_1 progeny were solid red. The F_2 population produced three distinct phenotypes. In addition to all red and all green plants, several of the green plants had considerable pigmentation on the petiole. He concluded that the two varieties differ by two dominant genes for pigmentation: one giving a red stem and petiole and the other affecting only the petioles.

Park and Rotar (1968) also found in Desmodium Sandwicense E. Mey that stem color was controlled by a single pair of genes with red dominant and green recessive. They found linkage between stem color and flower color in the coupling phase with an average recombination value of 34%. There were also differences in red intensity ranging from dark red to light red. No attempt was however made to determine mode of inheritance for this color modification because of difficulty in scoring shades of stem color. They did not observe complementary gene action for stem pigmentation.

Rotar and Kuan-Hon Chow (1971) working on the genetics of three species of Desmodium found that their stem color fell into three categories: red, brown and green. In determining genetic ratios Rotar and his colleague found that the stems were segregated into two

classes: (1) red or brown (2) green. Their results indicate that stem color in the three species is controlled by a single gene pair with dominance for red or brown stems and recessiveness for green stems. They also observed differences in intensity of the red stem color.

Genetic studies on stem color have not been reported as extensively as flower color. Park and Rotar (1968) felt this is partly because pigmentation and its intensity are sensitive to light intensity and age of stems. However, many studies have shown a monogenic inheritance of pigmented versus green stems with dominance for pigmentation.

Culp (1960) did report a case in which the green color of sesame plant was dominant to the purple stem color. He observed a ratio of 3 green : 1 purple in the F_2 progenies. A backcross to the purple parent however did not yield a 1 : 1 ratio. These results could not be explained.

Inheritance of Petiole Color: Investigation by Hofmyer (1938) revealed that in C. papaya purple petiole was dominant to green. He also observed differences in the intensity of the purple. This aspect was however not investigated further.

Angell and Gabelman (1970) found similar results in their study of inheritance of purple petiole in carrot, Daucus carota var sativa. These workers found dominant monogenic control of purple petiole over green. They also observed variations in intensity of purple in both green house and field studies. They concluded that this was suggestive of the presence of modifier genes in addition to a major gene

controlling the presence or absence of anthocyanin in the petioles. In the presence of the dominant allele, modifier genes apparently control the quantity of anthocyanin produced.

Inheritance of Ripe Fruit Color: Studies of inheritance of skin color of ripe fruits have not been reported in Carica. Inheritance of flesh color of papaya has been reported by Hofmyer (1938). He found red flesh color recessive to yellow. However, various studies done with the peppers, Deshpande (1933), Smith (1950), El Hassan and Smith (1970) showed red fruit color is dominant to orange, yellow and brown. Each of these colors was under the control of a single pair of genes. Smith (1950) also found that the relationship between brown and yellow was governed by two pairs of genes.

FLORAL BIOLOGY

Floral Anthesis: Sharma and Bajpai (1969) studied floral anthesis and anther dehiscence for C. papaya L. Their results indicated that anthesis started in the evening (5 - 8 p.m.) in all types of flowers. Petals took about twenty-four hours to completely unfold. An hourly observation of tagged mature flower buds showed maximum number of flowers opening between 6 and 7 p.m. Studies conducted in March and November did not show any significant difference in time of opening between the two periods. The period between flower bud appearance and anthesis was about eighty days. Anther dehiscence occurred about six hours prior to floral anthesis. Temperature and humidity were found to exert pronounced influence on anther dehiscence. High temperature and low humidity hastened the time of dehiscence while low

temperature and high humidity not only delayed the time but also slowed down the rate of dehiscence. It was also observed that slight variation in atmospheric temperature and humidity did not influence the rate of anthesis. Similar observations have been reported by Dasarathy (1951) and Balsabramanyam (1959) in Psidium guajava, Singh (1954) and Randhawa and Damodaran (1961) in Mangifera indica and Seaton and Kramer (1939) and Singh (1950) in cucurbits. However, similar work done on sweet lime by Singh and Dhuria (1960) and on plum by Randhawa and Nair (1960) showed that atmospheric temperature and relative humidity had promotive effect on floral anthesis. These authors found that higher temperatures combined with low humidity hastened the time of opening and increased the number of buds which opened. Flowers on shaded side of the tree opened later than those on the side exposed to the sun. Studies of floral anthesis in Acerola, Malpighia glabra L. conducted by Yamane and Nakasone (1961) showed that floral anthesis in this species was related to temperature. Flower buds which normally opened within twenty-four hours failed to open when placed in water at 58°F. Anthesis was however hastened when the buds were placed in water at 62 to 64°F. Low night temperatures were found to delay complete opening of flowers by two to three hours.

Pollen Viability in Vitro: Pollen germination and compatibility studies are useful in plant breeding, particularly when species and interspecific hybridizations are involved.

Traub and O'Rork Jr. (1936) germinated papaya pollen in vitro over a wide range of sucrose concentrations (1.0 - 8.0%) with 0.5 to

0.75 percent agar. They recommended a medium comprising 0.75 percent agar and 4.0 percent sucrose. Singh (1959) reported maximum germination of papaya pollen (67.6%) in 5.0 percent sucrose solution with one percent agar. Sharma and Bajpai (1969) also reported that five percent sucrose solution produced the best results in germination of papaya pollen in vitro. Allen (1963) also used 0.75 percent agar and 4.0 percent sucrose in germinating papaya pollen. Allen's study showed that germination of papaya pollen in vitro gave a reliable indication of germination in vivo. Kwack (1965), using the Brewbaker and Kwack's solution (1963), examined pollen growth for twenty-five species including C. papaya. He obtained maximum germination (80.5%) for the pollen of C. papaya at pH 8.3. It has been reported by Kwack (1964 and 1965) and Hirano and Nakasone (1965) that pH of the medium affects pollen germination.

INTERSPECIFIC HYBRIDIZATION

A number of interspecific crosses have been made in the genus Carica. It is probable that considerable natural hybridization has also taken place in the genus. Carica x heilbornii is said to have originated as a natural hybrid between C. pubescens and C. stipulata, (Horovitz and Jimenez, 1967). This plant which sets fruits parthenocarpically, is propagated by cuttings. Higgins and Holt (1914) also reported what was believed to be a natural hybrid between C. papaya and C. peltata in the orchards in Hawaii. These same authors claimed that the following interspecific crosses had been successfully made: C. cundinamarcensis x C. papaya, C. cauliflora x C. papaya,

C. erythrocarpa x C. cundinamarcensis and C. papaya x C. gracilis. Warmke et al. (1957) succeeded in making a cross between C. goudotiana and C. monoica using the latter as the pollen source. The reciprocal cross however failed to take. Sawant (1957) studied crossing relationships among C. papaya, C. monoica, C. goudotiana and C. cauliflora. He obtained viable seed in 2 out of 10 reported crosses. The fertile crosses were C. monoica x C. cauliflora and C. goudotiana x C. monoica.

Unsuccessful attempts at interspecific hybridization have been reported in the following cases: C. papaya x C. candamarcensis, C. papaya x C. quercifolia and C. papaya x C. hastaefolia (Higgins and Holt, 1914, Traub et al., 1942). Wolfe and Lynch (1940) reported failure of crosses between Jacaratia dodecaphylla and C. papaya using the latter as a female parent. Swingle (1947) also reported failure to obtain crosses between C. papaya and C. monoica.

Although Higgins and Holt (1914) reported success of a cross between C. cauliflora and C. papaya, more recent attempts to make this cross have not however been successful. Jimenez and Horovitz (1958) attempted crosses between six species of Carica. On the basis of crossability these authors arranged the six species in three groups. Group I included C. monoica, C. cauliflora, C. microcarpa and C. candamarcensis. These four species crossed fairly easily with each other and produced viable seeds. C. papaya and C. goudotiana were placed in Group II and Group III, respectively. Jimenez and Horovitz claimed that crosses between species in Groups I and II do not form mature seed but in many cases the immature embryos can be cultured. Crosses between Groups II and III always give negative results.

Attempts to incorporate the genes for resistance to "Distortion Ring-spot Virus" into C. papaya by crossing it with resistant species such as C. pubescens, C. stipulata and C. candicans have also failed because of cross incompatibility (Horovitz and Jimenez, 1967).

Jimenez (1957) reported that C. papaya, C. monoica, C. candamarcensis, C. cauliflora and C. goudotiana could be easily grafted on each other giving good vegetative growth. Appearance of male inflorescence on the graft of C. goudotiana on C. cauliflora caused both stock and scion to decline abruptly. Vigorous growth was however restored by removal of the flowering branches.

HETEROSIS

A species in which heterosis has been extensively studied is maize. In maize, the first studies on artificial hybridization for which yields were reported were those of Beal in the period 1877 - 1882, (cf. Allard, 1960). Beal made hybrids between different open pollinated maize varieties and although he did not give detailed data, he did state that yields of the hybrids were larger than those of the parents by as much as 40 percent.

The data of Robinson et al. (1956) based on replicated experiments conducted at three locations for two seasons gave a more accurate picture of the precise degree of heterosis in varietal hybrids of maize. In this study twelve out of fifteen crosses exceeded their high parent in yield and the mean of all hybrids relative to their high parent was 111.5 percent.

Responses to hybridization in other species are not as well known

as in maize. However, various degrees of heterosis have been reported in a number of species other than maize. These include the onion, Jones and Davis (1944), alfalfa, Tysdal et al. (1942), cabbage, Odland and Noll (1950) and Arachis hypogaea, Parker et al. (1970) and Wynne et al. (1970). Several workers including Vandenberg and Matzinger (1970) have also reported the exhibition of hybrid vigor in certain intervarietal hybrids of Nicotiana tabacum. Intervarietal crosses in self-pollinated species such as rice, wheat, beans and tomatoes have also been reported to exhibit various degrees of heterosis.

Santhanam (1952) studied the behavior of three interracial hybrids in Gossypium arboreum L. Among the productivity characters studied, consistent trends towards increase in the number of bolls produced and yield of 'Kapas' were observed in the F_1. One of the hybrids (N. M. Dollar x Cernuum) exhibited significant heterosis in both boll production and 'Kapas' yield while another hybrid (C 19 x Cernuum) showed significant heterotic effect in 'Kapas' yield only.

Muhammad et al. (1969) also reported some degree of heterosis in the castor oil plant, Ricinus communis L. In this study top crosses were made between six castor inbreds. Certain hybrid progenies were found to show heterosis in terms of number of days to flowering, number of capsules per raceme and yield. No heterotic superiority was observed in oil content and seed weight.

In Carica the only species which has been extensively bred is C. papaya L. In this species reports concerning heterosis or its converse inbreeding have been conflicting. Traub et al. (1942) presented a report on papaya breeding in the United States since 1932. These

workers stated that evidence was found suggesting deleterious inbreeding effects on pollen germination and vigor of young seedlings. It was claimed that a cross between two inbred lines, Orlando x Fairchild gave more vigorous progeny than that from selfed parents. No data were given to substantiate these claims. In discussing a series of good inbred solo lines under test at the University of Hawaii, Storey and Kamemoto (1947) also mentioned a loss of vigor in inbred lines.

Hofmyer (1953) in his report on sex reversal in C. papaya came to the conclusion that in some families the frequency of sex reversal was higher the longer inbreeding continued. He remarked that in the early generations only one stamen may develop in one or two flowers of a female plant, but with continued inbreeding the number of stamens gradually approached five. He did add however, "Inbreeding as such is not responsible for sex reversal, but it merely acts as an instrument to reveal any latent tendencies for sex reversal". He went further to suggest that inbreeding depression which can only be restored by crossing unrelated inbred lines also applies to papayas.

Stambaugh (1960) gave an account of forty years of papaya development in Florida and noted that hermaphrodite strains that were selfed beyond the third generation tended to deteriorate rapidly in their fruit bearing and seed producing habits.

A number of other workers did not find any evidence of heterosis or inbreeding depression in papayas. Hofmyer in one of his earlier papers (1941) reported on progeny studies with dioecious papayas in South Africa. He stated, "Although some of our dioecious varieties

have been inbred for five generations by sib pollination, the reduction in vigor is hardly noticeable". Hamilton (1954) conducted a quantitative study of growth and fruiting in inbred and crossbred progenies from two Solo papaya strains. In studying hybrid vigor and inbreeding effects with regard to earliness, stem diameter, terminal growth and height of bearing, Hamilton made the following comparisons:

1. selfed progenies of parental plants with their F_2 progeny;
2. mean of self progenies compared with that of cross progenies; and
3. mean of all interstrain crosses with the mean of all intrastrain crosses and selfs made among parental plants of each strain.

These comparisons did not show differences indicative of hybrid vigor. The F_1 mean either fell between parental means or was approximately equal to one parental mean. The means of four hermaphrodite self progenies did not differ significantly from the means of their respective hybrid progenies. He concluded that "neither loss of vigor from inbreeding nor hybrid vigor in F_1 plants was suggested by results of this progeny test".

Similarly, Nakasone and Storey (1955) conducted a study of quantitative inheritance of growth and fruiting characteristics of papaya. These authors made use of crosses of male and female plants from the Betty variety with hermaphrodites from the Line 5 Solo strain. The progeny tests included both parental types, the F_1, and F_2 and backcrosses of the F_1 to both P_1 and P_2. No evidence of hybrid vigor was detected in comparing the F_1 with the F_2.

SEX INHERITANCE

Much work has been done on sex inheritance in the genus Carica. Majority of the reports however concern C. papaya, the only species of any economic significance in the genus. Higgins (1916), Higgins and Holt (1914) and Kulkarni (1915) recognized up to 15 different sex types in C. papaya. Hofmyer (1938) and Storey (1941) however pointed out that each of the tree forms properly belongs to one of three basic sex types: staminate, hermaphrodite and pistillate. The pistillate (female) is the most stable sex form. The males and hermaphrodites show variations in sex expression under different environmental conditions.

Storey (1940) designated the trees by four sex forms: Form A (female), Form B (seasonally female-fertile staminate), Form C (continuously fertile harmaphrodite), Form D (male). Genetic studies carried out by Storey (1938) and by Hofmyer (1938) showed that each sex form remains an entity in inheritance. Both authors working independently came out with similar sex ratios in progenies of crosses between various sex forms. These ratios were explained on a factorial basis by assuming that maleness is determined by the dominant factor M_1, femaleness by a recessive factor, m, and hermaphroditism by a dominant factor M_2. Hence the staminate plant is genotypically M_1m, pistillate is mm and hermaphrodite is M_2m. The factors M_1, M_2 are assumed allelic and this is supported by the apparent lethality of double dominants, M_1M_1, M_2M_2 and M_2M_1.

In general, flowering plants show great diversity and complexity in their mechanisms of sex determination. This is borne out by the

numerous examples compiled by Westergaard (1958) in his article on mechanism of sex determination in flowering plants. A number of interesting phenomena are revealed in Westergaard's paper. In the genus, Ecballium (Cucurbitaceae) the species Ecballium elaterium has two varieties: Ecballium elaterium var monoicum and Ecballium elaterium var dioicum. The former is monoecious while the latter is dioecious. The results of extensive intercrossing between these two varieties were published by Galan (1950, 1951; cf. Westergaard, 1958). The results indicated that when intracrossed, the monoecious type produced monoecious offspring only and the dioecious species gave males and females in equal proportions. Results of intervarietal crosses showed two different patterns in the F_1 hybrids: when a female gamete from the dioecious variety was fertilized by a gamete from the monoecious type, all F_1 hybrids were monoecious. However, when a female gamete from the monoecious type was fertilized by a gamete from the dioecious type, the F_1 populations consisted of male and monoecious plants in equal proportions.

In Bryonia, when a female gamete from the dioecious species was fertilized by a gamete from a monoecious species F_1 hybrid plants were female. Crosses involving Acnida tamariscia (dioecious) and Amaranthus species (monoecious) produced two different patterns of sex expression in the F_1 hybrids. In some of these crosses all the F_1 hybrids were female plants and in the other crosses all the F_1 plants were males. These crosses have been classified as "1 - type" and "2 - type" respectively (cf. Westergaard, 1958). These are only a few of the many recorded examples in which crosses of dioecious males and females

with monoecious species have shown a very polymorphic pattern of sex determination.

With regard to wild species of Carica the first report on sex inheritance was by Warmke et al. (1954). Warmke and his associates found all F_1 plants of the cross Carica goudotiana x C. monoica to be monoecious like C. monoica. Sex segregation ratio among F_2 plants indicated a complex inheritance pattern. This was attributed to the fact that the fruits resulted from open pollination and could therefore have been fertilized with C. monoica or C. goudotiana pollen.

Later studies conducted by Horovitz and Jimenez (1967) produced significant results. These authors found that a cross between C. cauliflora and C. monoica using the latter as a male parent produced only monoecious F_1 plants. F_2 population segregated in a ratio of 3 monoecious : 1 female. Backcrossing to the cauliflora female parent produced 50% females and 50% monoecious plants. Horovitz and Jimenez concluded that this cross and the one reported by Warmke (1954) corresponded to the Ecballium type of Galan described by Westergaard. The Bryonia type of sex determination also mentioned by Westergaard was however detected by Horovitz and Jimenez in other crosses involving C. monoica (as male parent) and any of the following species as a female: C. pubescens, C. stipulata, C. microcarpa and C. horovitziana. The F_1 plants of these crosses were all females and backcrosses to the monoica parent yielded female and monoecious plants in equal proportions.

CYTOLOGY AND CYTOGENETICS

A number of cytological studies have been conducted on C. papaya. Studies undertaken by Lindsay (1930), Hofmyer (1938) and Storey (1941) have shown that the diploid chromosome number of C. papaya is 18. These studies did not however suggest heteromorphism in a chromosome pair either among somatic chromosomes or among chromosomes in various stages of meiosis. Kumar et al. (1945) reported however that one pair of chromosomes separates precociously at anaphase I of meiosis in male and hermaphrodites. No such separation was observed in the female. It was therefore concluded that the difference in behavior noted was in keeping with what had been observed in other species of plants which have heteromorphic sex chromosomes. No morphological differences between disjoining homologues were however detected.

This type of precocious separation was also observed by Storey (1953). Storey did not find this separation in every cell but stated, "precocious anaphasic separation may indeed be a feature which serves to set the sex chromosomes apart from the autosomes but further studies would be required to determine with certainty which one of the 9 pairs behaves in this way and whether a means might be discovered to distinguish the disjoining sister chromosomes from each other".

Heilborn (1921, cf. Kumar et al., 1945) first conducted cytological work on other species of Carica. Heilborn studied the cytology of C. chrysopetala, C. pentagona and C. pubescens. He found the diploid number of chromosomes in all of these to be 18. Several other species including C. cauliflora, C. peltata, C. pubescens, C. dodecaphylla and C. quercifolia have been examined cytologically (Storey, 1941, Kumar,

1942, 1944, cf. Chromosome Atlas, 1956). It has also been reported that C. goudotiana, C. monoica and C. microcarpa have been studied cytologically (cf. Zerpa, 1959). In all of these studies the diploid number of chromosomes was found to be 18.

The majority of interspecific hybrids so far produced in this genus, Warmke (1954), Horovitz and Jimenez (1967) have been fertile. Studies of microsporogenesis of six of the hybrids conducted by Zerpa (1959) revealed that all hybrids were diploid with 18 chromosomes. Meiotic pairing and bivalent formation were normal except in the case of C. cauliflora x C. candamarcensis which formed some multivalents.

MATERIALS AND METHODS

CONTROLLED POLLINATION TECHNIQUE

All the species under investigation except C. monoica and C. papaya are dioecious. Controlled sib pollinations and interspecific crosses were made in all possible combinations. All pollinations were done at the mature bud stage. In all cases in which C. monoica was used as a female parent, the raceme was stripped of all staminate flowers leaving only the terminal pistillate flower bud to be pollinated. Where hermaphroditic flowers of C. papaya (cv. Solo) were involved, hand emasculation was done before anther dehiscence.

The controlled pollination techniques currently used in papaya breeding in Hawaii were adopted for these studies. All pistillate flower buds pollinated were the ones due to open within a day. These could be selected on the basis of size and petal color changes. Where hermaphroditic papaya flowers were to be pollinated less mature buds were used to ensure that pollen was not shed before emasculation was done. All staminate flower buds as well as hermaphrodites usually shed pollen before anthesis. The mature staminate flower buds to be used as sources of pollen were selected also on the basis of size and color changes.

Before effecting pollination, the staminate bud was stripped of its petals. The pistillate flower bud was then opened by hand and the remaining part of the staminate flower was used as a brush in dusting the pollen on the stigmatic surface. A small glassine bag was immediately slipped over the pollinated bud. The bag was then firmly tied

around the flower stalk with a string attached to a metal rim label upon which was recorded the index numbers of the parental species involved in the cross and the pollination date. Both bud pollination and bagging ensured the prevention of contamination by foreign pollen.

CULTURAL METHODS

Seed Germination: Seeds were germinated in plastic pots, using vermiculite as the germinating medium.

Handling of Seedlings: When seedlings had reached the 2 - 4 leaf stage they were transplanted individually into three-inch jiffy pots. The medium in the jiffy pots consisted of sterilized top soil, sponge-rok and peat moss in the ratio of 2 soil : 1 sponge-rok : 1 peat moss. A small hole was made at the bottom of each jiffy pot to facilitate draining of excess water. Seven days after transplanting into jiffy pots a "pinch" of orchid organic fertilizer was given to every seedling. Routine watering and fertilization of seedlings in jiffy pots were continued for about eight weeks. By this time seedlings had attained a height of about six inches.

Field Planting: Seedlings were transplanted into the field at the University of Hawaii Experimental Station at Waimanalo. Field preparation involved the routine operations of plowing, discing and running irrigation furrows ten feet apart. To minimize the effect of the "replant problem" soil was treated with captan at the rate of 40 lbs. per acre when replanting after the first time. Planting was done on the basis of one seedling per hole with the jiffy pots intact. Spacing

was five feet between plants and ten feet between rows. Individual progenies were planted consecutively. Furrow irrigation was carried on as necessary, usually once a week except when there was excessive rainfall. The following fertilizer schedule was adopted:

Two weeks after planting	½ lb. of 10-10-10 per seedling;
Two months after planting	1 lb. of 10-10-10 per tree;
Four months after planting	1 lb. of 10-10-10 per tree;
At flowering and fruiting	2 lbs. of 10-10-10 per tree every three months.

Weed control and spraying for insects and diseases were undertaken whenever necessary.

BIOLOGICAL DATA

Pollen Germination in Vitro: In these studies pollen germination in vitro was conducted on an agar medium using Brewbaker and Kwack's (1963) solution at six different pH levels (4.5, 5.5, 6.5, 7.5, 8.5, 9.5). The composition of Brewbaker and Kwack's solution is as follows: calcium nitrate (300 ppm), magnesium sulfate (200 ppm), potassium nitrate (100 ppm), boric acid (100 ppm) and sucrose (10 percent). Kwack (1965) had shown that the concentrations of the various ions were near optimum for pollen germination of a number of species including C. papaya.

The stock solution used in these investigations was prepared on the basis of parts per liter. Appropriate weights of the salts that is,

calcium nitrate (0.3 gm.), magnesium sulfate (0.2 gm.), potassium nitrate (0.1 gm.) and boric acid (0.1 gm.) were dissolved in 250 cc of warm distilled water. The solution was then made up to one liter. The 10 percent sucrose stock solution was prepared separately.

Pollen was germinated in petri dishes. About 200 cc of the stock solution was used in every test. The pH of the solution to be used was then adjusted with 1N KOH or 1N HCl to the required level. About one gram of agar was then added and the mixture was heated to boiling. The mixture was constantly stirred until all the agar had dissolved. The hot mixture was then poured into a number of clean petri dishes and allowed to set. As soon as the medium had set firmly, 10 percent sugar solution was used in rinsing the surface of the medium. Excess sucrose solution was decanted off.

Fresh pollen was collected immediately before each germination test. The pollen used was from mature staminate buds. The petals were removed and the pollen was spread evenly over the surface of the medium. Each petri dish was then covered and labeled according to the species from which the pollen was collected. The petri dishes were arranged in rectangular plastic troughs which were then kept in the laboratory air-conditioned at about $24^{o}C$.

Counting of germinated pollen was done after about twenty hours under light microscope using a hand counter. Germinating pollen from four random microscopic fields was counted per dish and the averages taken. Each treatment was replicated four times.

Length Measurements: Lengths of leaves and flower buds were measured as a means of showing morphological differences between plants. Length of flower buds was measured to the nearest 0.05 cm. Only the mature or ready-to-open flower buds were measured. The length measured was the distance from the base of the receptacle to the apex of the folded petals. A pair of calipers was used for this measurement. Raceme length and leaf length were both measured to the nearest 0.5 cm. Leaf length was taken as the distance from the leaf base to the apex of the lamina. Five fully formed leaves were detached from each tree. The leaves were taken from different sides of the tree. Measurement was done with a measuring tape. Averages were then compiled for each tree.

Fruit Shape Determination: Fruit shape was determined by means of an index. Indices were compiled as follows: the length and diameter of the fruit were measured to the nearest 0.5 cm. The ratio $\frac{\text{length of fruit}}{\text{diameter of fruit}}$ was taken as the fruit shape index.

Color Determination: Fruit, stem and petiole colors were determined by visual observations as well as by Horticultural Color Chart (Robert F. Wilson, 1941). Fruit color was scored only for ripe fruits.

Floral Biology: The time from flower bud appearance to anthesis was determined by tagging immature leaves as soon as the young flower buds became barely visible at their axils. The dates of tagging were duly recorded. The time from flower bud appearance to the opening of the flower and sex of flower were recorded.

The time of floral anthesis was determined by tagging mature buds

of all sex types and making observations at two hour intervals from 6 a.m. to 10 p.m. The plants used in this investigation (except C. papaya) were those planted in five-gallon cans. For C. papaya, field-planted trees on the Manoa Campus were selected for this purpose.

Measurement of Heterosis: Heterotic effects were studied using two single crosses involving three species. C. goudotiana (149R) and C. cauliflora (145), both of which are dioecious species were perpetuated by controlled sib-pollinations for two consecutive generations. At the same time C. monoica, a monoecious species was inbred for two generations. All the three parental species were found to breed true to type. C. cauliflora and C. goudotiana were found to be cross incompatible but both were cross fertile with C. monoica, using the latter as a male parent. Consequently the two crosses used in the study of hybrid vigor were C. cauliflora x C. monoica and C. goudotiana x C. monoica.

Seedlings of the three parental species and those of the two F_1 hybrids were field-planted at Waimanalo Experimental Station in November 1970. Seedlings were uniform in size and appearance at transplanting time. Plants were given the same cultural treatments throughout the course of this investigation.

Vegetative characters, yields and fruit characters were studied to determine the presence of heterosis. The vegetative characters studied were tree height and trunk circumference of eight-month old trees. These characters had been cited as evidence of good vigor in the selection index for papaya breeding, (Agnew, 1941). Height of

trees was measured to the nearest centimeter using a measuring rod. The measurement of trunk circumference was done to the nearest cm. at a level one foot above ground, using a measuring tape.

Yield per tree was determined for the first crop only. Yield for the first crop is defined as the number and weight of all fruits set on the tree at the time the first fruits began to ripen. The number of fruits was counted by means of a hand counter. Average fruit weight was obtained by weighing twenty-five ripe fruits per tree. The average weight per fruit was then multiplied by the total number of fruits on the tree to get the total weight of the first crop. This was done for the parents and the F_1 hybrids.

Data were subjected to analysis of variance using the F-test for the comparison of two independent samples, (cf. Snedecor and Cochran Statistical Methods 6th Edition). To compare generations, the error variance used in the analysis of variance was within generations. The F value was the ratio of between and within variances. The total variance for all plants was computed and the variance due to generations was subtracted from the total. The remainder was divided by degrees of freedom for within generations and this provided an estimate of error variance. (See Tables XII and XIII under results.)

Genetic Studies: The following characteristics were used in genetic studies:

(a)	Stem color	red vs. green
(b)	Leaf petiole color	red vs. green
(c)	Fruit color	red vs. yellow
(d)	Flower color	white vs. pale yellow; pale yellow vs. purple-blush
(e)	Sex forms	monoecious vs. dioecious
(f)	Fruit configurations	grooves vs. ridges; wide grooves vs. narrow grooves
(g)	Fruit pulp	succulent vs. dry
(h)	Branching	sparse vs. bush branching
(i)	Seed coat	spiny vs. non-spiny

Cytology: Cytological studies were made using pollen mother cells. McClintock's (1929) Acetocarmine method was modified and used for this investigation. Aceto-orcein was substituted for acetocarmine. Chloroform was added to Carnoy's solution and used as the fixative.

Immature male flower buds about 0.5 cm. long were collected and stripped of their petals. The anthers were then placed directly in a small vial bottle containing the fixative (three parts of absolute alcohol, one part of chloroform and one part of glacial acetic acid). The anthers were kept in the fixative for twenty-four hours in an air-conditioned room.

Anthers were then washed with tap water and transferred to a drop of aceto-orcein on a microscope slide. The contents of the anthers were carefully teased out and all debris was removed. A cover slip was

then placed over the specimen. Excess stain was removed by placing a blotter at the edge of the cover slip. Cover slip was not thumb-pressed to spread the cells. Preliminary preparations in which cover slip was pressed by thumb did not yield good results because pollen mother cells were fragmented. The slide was warmed over an alcohol flame intermittently until the cells were flattened and spread. Slides were then examined under the light microscope for different stages of meiosis at x 1500 magnification.

Plant Material: Nine Carica species, including C. papaya L. were used in these investigations. The species under investigation, their Index numbers and sources are shown in Table I.

TABLE I

List of species investigated, their index numbers and sources

Index Number *	Species	Source
125	Carica pennata Heilborn, Svensk	Costa Rica
131	Carica parviflora (A.DC.) Solms.	Venezuela
145	Carica cauliflora Jacq. A	El Salvador
149R	Carica goudotiana (Red) (Tr. & Pl.) Solms. AR	Colombia
149Y	Carica goudotiana (Yellow) (Tr. & Pl.) Solms. AG	Colombia
194	Carica cauliflora Jacq. B	Venezuela (only females represented)
133	Carica horovitziana Badillo	Venezuela
195	Carica goudotiana Jacq. B	Venezuela
198	Carica monoica Desf.	Venezuela
203	Carica species	Colombia (only females represented)
140	Carica pubescens Lenne et Koch	Venezuela
$26F_4$	Carica papaya L. (Inbred hermaphrodites)	
$5BF_{12}$	Carica papaya L. (Inbred hermaphrodites).	

* Refers to numbers given to species in Nakasone's collections.

Carica goudotiana: Carica goudotiana Planch and Triana is a dioecious species. Under the conditions of the experiment the plants grew to an average height of 1.96±0.10 meters in eight months. In eight months, trunk circumference (1 ft. above ground level) reached an average of 29.21±0.87 centimeters. Trees were sometimes straight and unbranched but quite often they were moderately branched. Each leaf was deeply divided into five primary lobes and each lobe was subdivided into a number of secondary lobes. Average leaf length was 81.98±2.18 cm. The petioles and young parts of the stem had a red pigment which varied in intensity from light red through red to dark red.

Male inflorescence was much longer than female inflorescence. Male and female racemes were 37.11±1.02 cm. and 6.22±0.38 cm. long respectively. Flowers of both sexes had a green background with a tinge of purple. Female flowers averaged 2.69±0.38 cm. in length. Male flowers were 2.27±0.02 cm. long. Some female trees (149R) produced red fruits and others, (149Y and 195) produced yellow fruits. Each fruit weighed about 186.30±9.57 grams. Fruits were ridged and markedly pentagonal in cross-section. Fruits were somewhat elongated with an average fruit shape index of 1.74±0.03.

Three forms of C. goudotiana (149R, 195 and 149Y) were studied here. All of them were similar in their gross morphology. They differed only in degree of pigmentation in the stems and fruits. Fruits of 195 were smaller but actual measurements were not done before trees were destroyed.

Carica monoica (198): Under the conditions of the experiment C. monoica grew to an average height of 1.47±0.04 meters in eight months by which time its trunk circumference was 16.51±0.73 cm. Plants were profusely branched usually close to the ground level. Leaves were 36.68±0.69 cm. long and each leaf was three-lobed. Stems and petioles were green. C. monoica is clearly monoecious, each inflorescence usually consisting of one female flower at the terminal position, flanked at the lateral level by numerous staminate flowers. Lengths of male and female flowers were 2.28±0.01 cm. and 2.03±0.03 cm. respectively. Immature flowers were light green but became pale yellow at maturity. Fruits were orange in color and oval in shape with a fruit shape index of 1.51±0.02. Each fruit had five wide and shallow grooves and weighed 53.57±2.47 grams. Seeds were covered by numerous prominent "horn-like projections".

Carica parviflora (131): C. parviflora was the smallest of all the species studied. In eight months plants grew to an average height of 0.69±0.08 meters while average trunk circumference was 6.84±0.47 cm. Plants were straight and usually unbranched. Stem was green but petioles were tinged with a red pigment. Leaves were three-lobed and reached an average length of 27.67±1.40 cm. The species is dioecious. Male and female inflorescences were (14.79±0.53) cm. and 2.95±0.15 cm. respectively in length. Racemes and flowers were bright pink. Length of male flowers was 1.71±0.02 cm. and female flower length was 1.70± 0.03 cm. Ripe fruits were orange in color and conspicuously five-ridged. Fruits were elongated with an average fruit shape index of

2.41±0.07. Each fruit weighed 2.20±0.21 grams on the average.

Carica cauliflora (145): Under the conditions of the experiment, C. cauliflora plants attained an average height of 1.90±0.07 meters in eight months. In eight months, trunk circumference was 32.88±0.45 cm. Trees were usually straight and very seldom branched. Leaves and young stems were green. Leaves were markedly five-lobed and averaged 122.38±0.76 cm. in length.

Plants were dioecious. Flowers were borne both in the axils of young leaves and on bare tree trunk. Male racemes were 18.82±0.38 cm. long and female racemes averaged 4.90±0.18 cm. in length. Immature flowers were green but turned white when matured. Male and female flowers averaged 3.82±0.04 cm. and 3.76±0.03 cm., respectively in length.

Female plants produced yellow to orange fruits which were elongated. Fruit shape index was 2.05±0.03 and each fruit weighed 95.03± 2.23 grams on the average. Fruits had five narrow grooves running longitudinally from the anterior end to the posterior end of the fruit.

One other form of Carica cauliflora (194) was also used in the present studies. It was also a dioecious species but only the female plant was established here. Tree characteristics were similar to those of Index No. 145 but the latter was smaller in size and produced more elongated fruits than Index No. 194.

Carica pennata (125): Carica pennata is similar in general morphology and growth habit to C. cauliflora. In fact Badillo (1967) classified both plants as synonymous. However, in the present studies it was

found that these plants differed markedly with respect to length of male raceme as well as in fruit shape. The average male raceme length of C. pennata was found to be 43.73±2.63 cm. while that of C. cauliflora was 18.82±0.38 cm. Fruits of C. pennata were not as elongated as those of C. cauliflora. Fruits of C. pennata had a rounded apex as opposed to those of C. cauliflora which had a tendency to be pointed. Fruit shape index of C. pennata was 1.22±0.02 while that of C. cauliflora was 2.05±0.03. Average fruit weight of C. pennata was 85.77 grams.

Index No. 203: Introduced from Colombia, the specific name of this dioecious species was not known. Only a single female plant was established in a five-gallon can. Its field performance could not be determined. The plant was straight and unbranched. Young stem and leaves were green. Each leaf was five-lobed. Flowers were light green in color. Fruits were small, orange colored and tended to be round with a fruit shape index of 0.93 and average weight of 25.84 grams.

RESULTS AND DISCUSSION

Floral Biology: Floral biology was studied in five species and three interspecific hybrids which had been established on the Manoa Campus. Studies of time of floral anthesis were conducted on all the species (except C. papaya L.) in the month of March. Observations were made every two hours starting from 6 a.m. to 10 p.m. Similar studies were undertaken in C. papaya in April and observation time was extended to 12 midnight. A graphical presentation of the results is given in Figure 1. A perusal of Fig. 1 shows that all the species (except C. parviflora) showed peak anthesis between late afternoon and early evening. A few flowers opened between 10 p.m. and 6 a.m. but this number was insignificant. C. parviflora started anthesis shortly after 6 a.m. and continued until afternoon; peak anthesis occurring between 8 and 10 a.m.

Time of maximum anthesis of interspecific hybrids was closer to that of one of the parents. C. parviflora and C. goudotiana were directly opposite with respect to their time of maximum anthesis. C. parviflora (female) showed the majority of flowers opening between 8 and 10 a.m., while C. goudotiana (male) showed maximum anthesis between 4 and 6 p.m. The hybrid C. parviflora (female) x C. goudotiana (male) showed peak anthesis between 10 a.m. and 12 noon. It is probable the early opening of C. parviflora is dominant to the late opening of C. goudotiana. Crosses were made to obtain F_2 population but these had not matured by the time of this report.

Studies of the F_2 population of this cross may provide an interesting genetic analysis of time of anthesis. Where both parents showed maximum opening at approximately the same time, their hybrid also showed maximum opening at the same time. See Figures 1A to 1C.

The period between flower bud appearance and anthesis was also studied for some species and F_1 hybrids. A minimum of ten flower buds was tagged per species and the time (in days) it took each bud to reach anthesis was recorded. Averages per bud were then calculated and figures were corrected to the nearest whole number. The results of these studies are presented in Table II. Comparison of parents and their hybrids in three crosses revealed a general tendency of the hybrids to behave more like one of their parents. This tendency was however shown to a variable degree by the three hybrids. The flowers of the hybrid, C. goudotiana (female) x C. monoica, took 34 days to reach anthesis from bud appearance. This value was approximately equal to the midparental value with a slight edge of 0.5 day for the early parent. The flower buds of the hybrid C. cauliflora (female) x C. monoica took an average of 33 days between bud appearance and anthesis, a value which was one day earlier than the early parent. The hybrid of C. parviflora and C. goudotiana took 23 days to reach anthesis from bud appearance. This value was 4 days earlier than the early parent.

Flowers of C. papaya took a much longer time to reach anthesis from bud appearance than the other species used in this study. Staminate flowers showed a tendency to be slightly later in reaching anthesis than pistillate flowers. In C. goudotiana the male flower bud took

32 days while the female took 31 days to reach anthesis. In C. cauliflora, the staminate and the pistillate buds took 40 and 34 days respectively to reach anthesis from bud appearance. A similar trend was also shown by the hybrids. The hybrid, Index No. 203 x C. cauliflora took 36 and 32 days respectively for the male and female flowers to reach anthesis from bud appearance. In the hybrid, C. cauliflora x C. monoica, the pistillate flower was 12 days earlier than the staminate flowers. This 12 day difference is rather high. Perhaps the flowering habit of the plants had a lot to do with this. The plants were monoecious and both staminate and pistillate flowers were produced on the same inflorescence, with the pistillate flower nearly always occupying the terminal position. At the time of tagging when the flower bud was just visible in the leaf axil, it was really the apex of the incipient pistillate flower that was visible. It is likely the female flower started development much earlier than the male and consequently reached anthesis in advance of the male. Since the exact time of appearance of male flower buds on the same inflorescence could not be determined, calculations were done for both female and male flowers from the date of tagging.

Sharma and Bajpai (1969) found that it took the flower buds of all sexes of C. papaya L. vars Coorg and Honey Dew about 80 days from bud appearance to anthesis. In the present studies it took 47 days for the hermaphrodite and 45 days for the female flower buds to reach anthesis from bud appearance. It would seem that the variety Solo, studied here matured much faster than the varieties reported by Sharma and Bajpai. It is also possible that differences between climatic conditions of

both areas could account for these discrepancies.

The precise time of anther dehiscence could not be determined. However, observations showed that all male flowers shed pollen as early as 48 hours prior to anthesis.

Results of time of anthesis obtained for C. papaya are in close agreement with those presented by Sharma and Bajpai (1969). These authors found that maximum number of flowers opened between 6 p.m. and 7 p.m. In the present studies maximum number of male and female buds were found to open between 6 and 8 p.m. while hermaphrodite flowers reached the peak of anthesis between 8 and 10 p.m. No differences were observed in time of anthesis between plants kept in the glass house and those kept outside. Sharma and Bajpai also did not find any differences in time and rate of anthesis due to slight variations in atmospheric temperature and humidity. Studies conducted on Psidium guajava (Dasarathy, 1951, Balsabramanyam, 1959), on Mangifera indica (Seaton and Kramer, 1939) and on Cucurbits (Singh, 1950) failed to detect any influence of atmospheric temperature and relative humidity on time and rate of floral anthesis. However, studies on plum (Randhawa and Nair, 1960) and on acerola (Yamane and Nakasone, 1961) revealed that atmospheric temperature and humidity had effect on time and rate of floral anthesis in some clones.

The majority of the flowers of C. papaya L. opened at night and most of the other species showed maximum number of flowers opening after 4 p.m. All species and hybrids studied produced pollen copiously. Pollen was powdery and easily wind-borne. Perhaps wind plays a major role in the pollination of these plants. C. parviflora reached peak

anthesis before noon. Its hybrid with C. goudotiana also showed maximum number of flowers opening between 10 a.m. and 12 noon.

The fact that time of anthesis and the period between bud appearance and anthesis of the hybrids were determined by those of the parents indicate these features are heritable and hence genetically controlled.

TABLE II

Period between flower bud appearance and anthesis in some Carica species and hybrids

Species/Hybrid	Sex of flower	Bud appearance to anthesis (days)
C. goudotiana	male	32
C. goudotiana	female	31
C. cauliflora	male	40
C. cauliflora	female	34
C. parviflora	female	27
C. monoica	male	38
C. papaya L. cv. Solo	hermaphrodite	47
C. papaya L. cv. Solo	female	45
C. goudotiana x C. monoica	female	34
C. cauliflora x C. monoica	male	45
C. cauliflora x C. monoica	female	33
C. parviflora x C. goudotiana	female	23
Index No. 203 x C. cauliflora	male	36
Index No. 203 x C. cauliflora	female	32

Figure 1A: Graphs of floral anthesis (percentage of flowers opened versus time of opening) of male and female flowers of Carica cauliflora and C. parviflora, (as labeled).

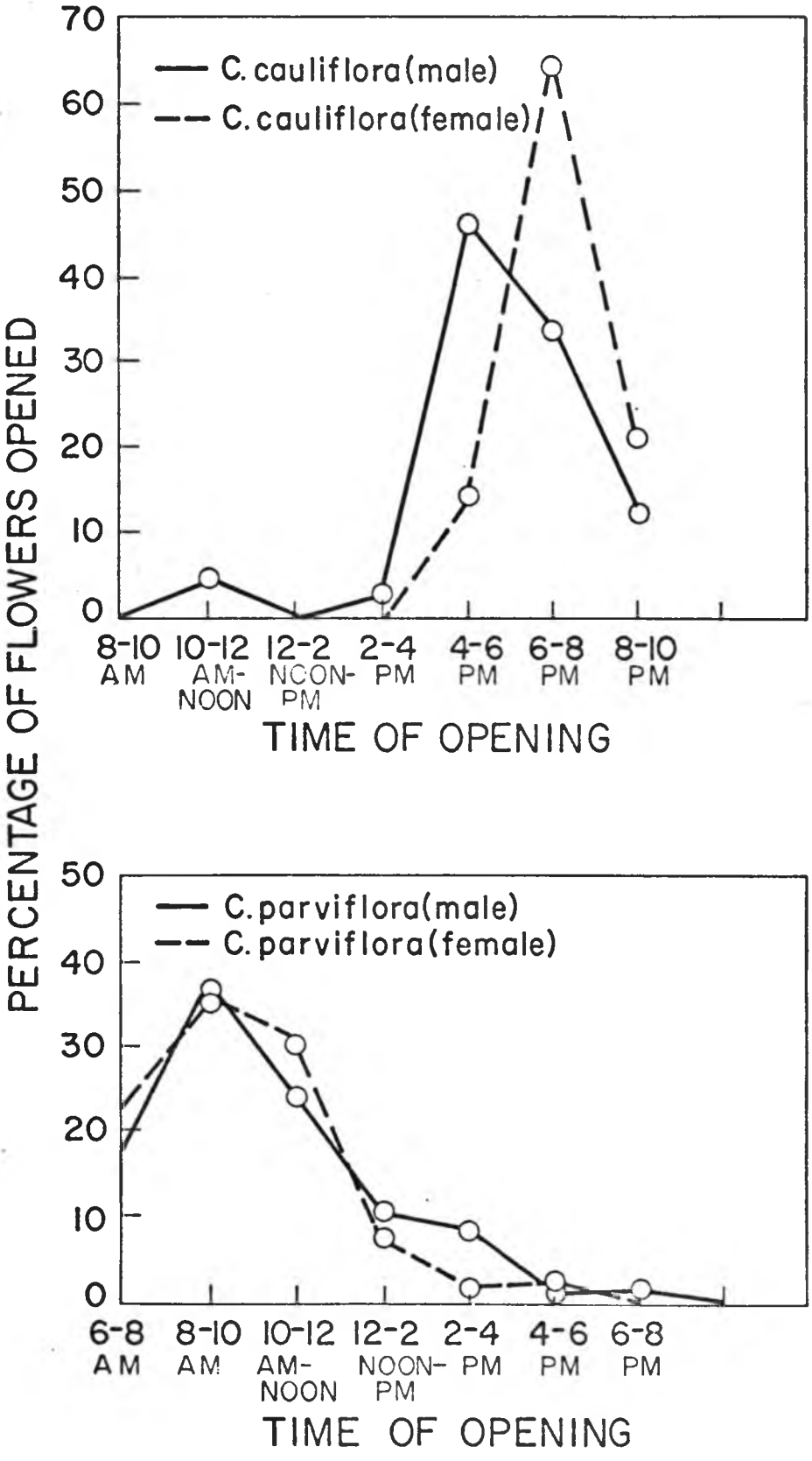

C. cauliflora(male)
C. cauliflora(female)
C. parviflora(male)
C. parviflora(female)
PERCENTAGE OF FLOWERS OPENED
70
60
50
40
30
20
10
0
8-10 AM
10-12 AM-NOON
12-2 NCON-PM
2-4 PM
4-6 PM
6-8 PM
8-10 PM
6-8 AM
8-10 AM
10-12 AM-NOON
12-2 NOON-PM
2-4 PM
4-6 PM
6-8 PM
TIME OF OPENING
TIME OF OPENING

Figure 1B: Graphs of floral anthesis (percentage of flowers opened versus time of opening) of male, female and hermaphroditic flowers of C. monoica, Carica papaya and C. goudotiana, (as labeled).

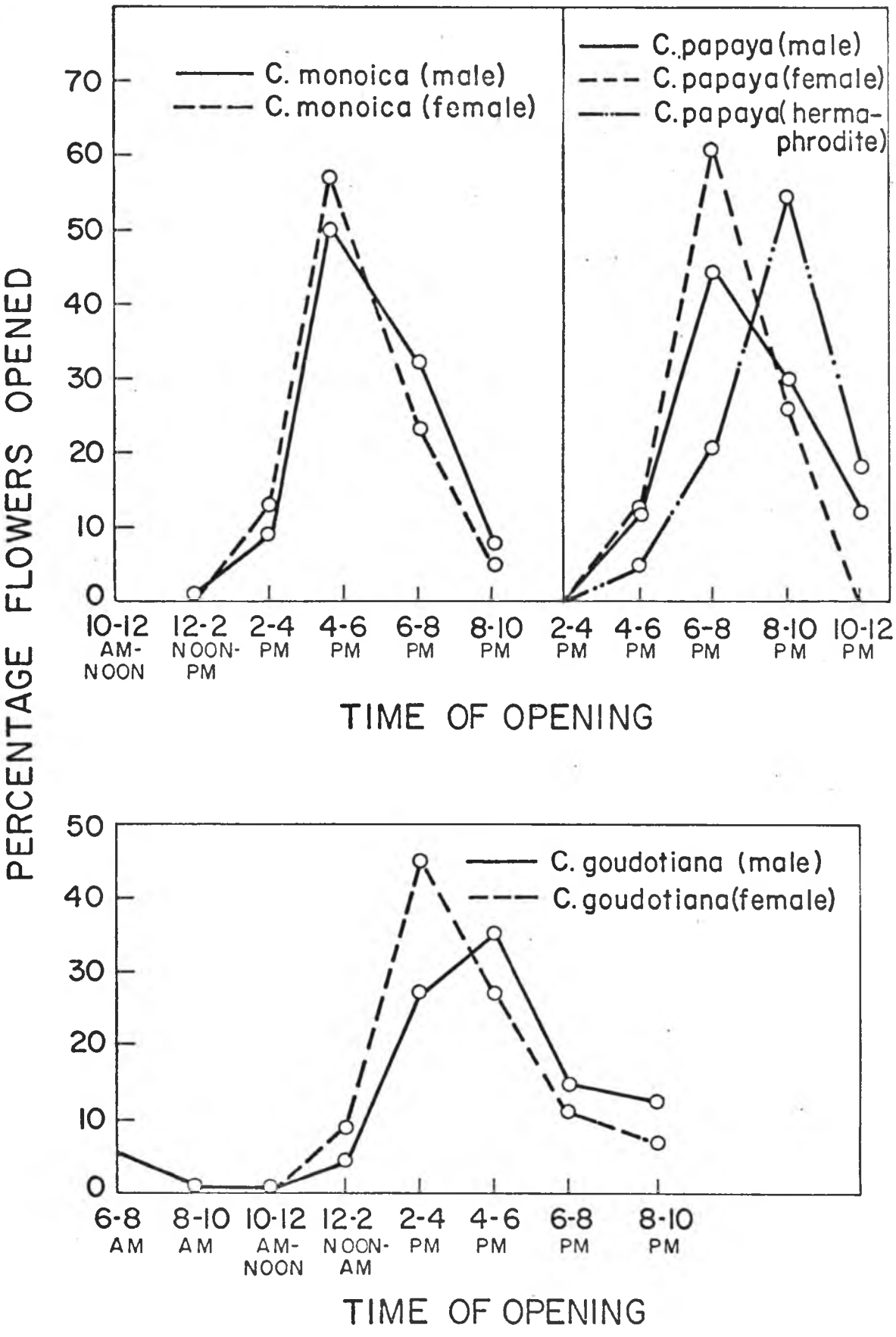
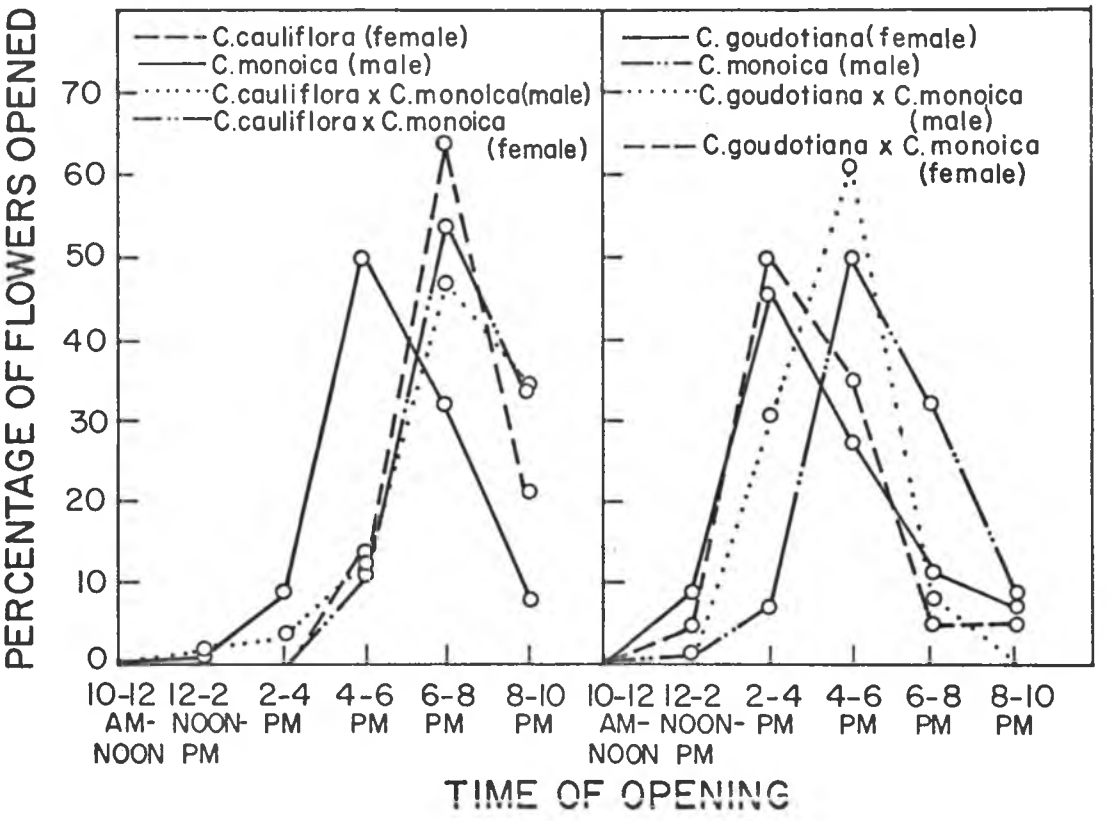
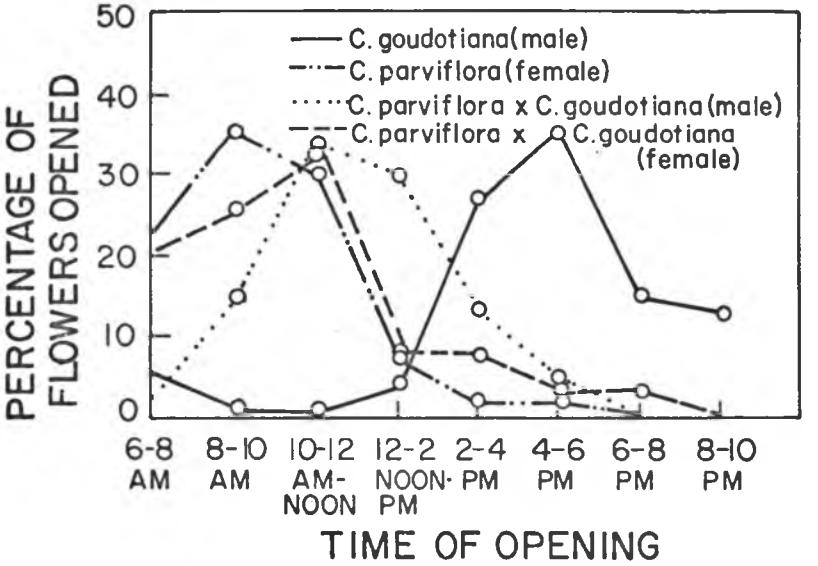

C. monoica (male)
C. monoica (female)
C. papaya (male)
C. papaya (female)
C. papaya (hermaphrodite)
PERCENTAGE FLOWERS OPENED
0
10
20
30
40
50
60
70
10-12 AM-NOON
12-2 NOON-PM
2-4 PM
4-6 PM
6-8 PM
8-10 PM
2-4 PM
4-6 PM
6-8 PM
8-10 PM
10-12 PM
TIME OF OPENING
C. goudotiana (male)
C. goudotiana (female)
0
10
20
30
40
50
6-8 AM
8-10 AM
10-12 AM-NOON
12-2 NOON-AM
2-4 PM
4-6 PM
6-8 PM
8-10 PM
TIME OF OPENING

Figure 1C: Graphs of floral anthesis (percentage of flowers opened versus time of opening) of male and female flowers of 3 Carica interspecific hybrids and their parental species, (as labeled).


C.cauliflora (female)
C.monoica (male)
C.cauliflora x C.monolca(male)
C.cauliflora x C.monoica (female)
C. goudotiana(female)
C. monoica (male)
C.goudotiana x C.monoica (male)
C.goudotiana x C. monoica (female)
PERCENTAGE OF FLOWERS OPENED
0
10
20
30
40
50
60
70
10-12 AM-NOON
12-2 NOON-PM
2-4 PM
4-6 PM
6-8 PM
8-10 PM
TIME OF OPENING


C. goudotiana(male)
C. parviflora(female)
C. parviflora x C. goudotiana(male)
C. parviflora x C. goudotiana (female)
PERCENTAGE OF FLOWERS OPENED
0
10
20
30
40
50
6-8 AM
8-10 AM
10-12 AM-NOON
12-2 NOON-PM
2-4 PM
4-6 PM
6-8 PM
8-10 PM
TIME OF OPENING

Pollen Germination in Vitro: In this work it was intended to study pollen germination in vitro only as a means of ascertaining whether any of the species produced non-viable pollen. The results of these studies are presented in Table III. Each value represents an average of four replications. Fig. 2 shows the graphical presentation of the same results.

All the species were found to produce pollen showing various degrees of viability under the conditions of the experiment. The viability shown by the pollen of each species was high enough to attribute any case of cross incompatibility to factors other than production of non-viable pollen. Allen (1963) presented evidence to show that germination of papaya pollen in vitro gave a reliable indication of germination in vivo. Germination was obtained over a wide range of pH levels. However, highly significant (5% and 1% levels) differences in percentage pollen germination at the different pH levels were indicated. A general trend showing a gradual rise in percentage germination of pollen with increase in pH from pH 4.5 up to pH 7.5 followed by a drop at pH 8.5 and pH 9.5, was observed in all the species. It would seem that in general lower pH levels (4.5 - 7.5) were more favorable to pollen germination than higher pH levels (8.5 - 9.5) in all the species investigated here. Kwack (1964, 1965), Hirano and Nakasone (1967) had shown that the pH of the germinating medium had profound effect on germination of pollen. The role of pH in pollen germination is not certain. Kwack (1965) suggested that pH effect might probably be associated with rigidity of the pollen wall. Perhaps enzyme activities are also affected.

Results of analysis of variance (F-test) run on the data are shown in Table IV. Results indicated marked differences in percentage germination of pollen of the different species. Pollen of C. goudotiana and C. papaya showed lower percentage germination than pollen of other species. Interaction between pH and species was significant at both the 5% and the 1% levels. Pollen of C. cauliflora and C. monoica showed a much wider adaptability to pH range than other species used in this study. Differences between replications were significant at the five percent level. The F-value for replications was 2.93 which was only 0.23 higher than the five percent level. This was indeed a border line case. It is probable that slight fluctuations in laboratory temperature during the course of the experiment produced this effect.

TABLE III

Results of pollen germination in vitro of six Carica species at six different pH levels

Species	Percentage germination observed					
	pH levels					
	4.5	5.5	6.5	7.5	8.5	9.5
C. goudotiana	24.86	36.23	45.94	47.65	4.38	0.76
C. parviflora	52.26	57.86	59.02	75.90	38.90	14.44
C. cauliflora	86.96	88.92	93.21	86.96	68.40	32.33
C. pennata	56.80	75.08	78.47	54.87	39.31	21.62
C. monoica	70.51	89.16	93.39	90.66	73.86	20.88
C. papaya	49.95	54.60	55.10	59.76	10.78	7.31

TABLE IV

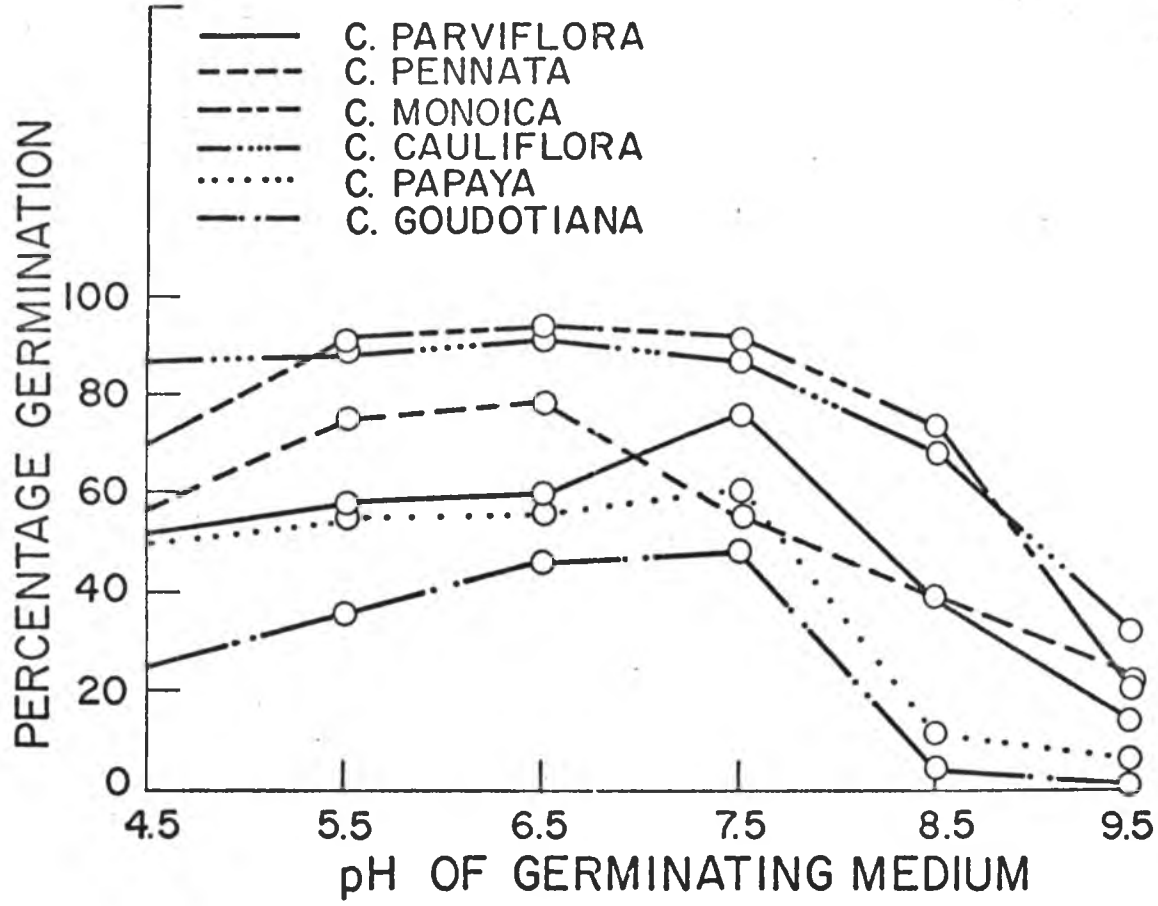
Analysis of variance of percentage germination of pollen in vitro of six Carica species at six different pH levels

Source of variation	D.F.	SS	MS	F
Total	143	112112.86		
Replications	3	385.88	128.63	2.98 *
Species	5	43806.32	8761.26	199.80 **
pH levels	5	56057.64	11211.53	255.68 **
Species x pH	25	7259.13	290.37	6.62 **
Error	105	4603.89	43.85	

* Significant at the 5% level

** Significant at the 1% level

Figure 2: Graphs of pollen germination in vitro for six Carica species; percentage germination observed plotted against pH of germinating medium (Brewbaker and Kwack's solution).


C. PARVIFLORA
C. PENNATA
C. MONOICA
C. CAULIFLORA
C. PAPAYA
C. GOUDOTIANA
PERCENTAGE GERMINATION
100
80
60
40
20
0
4.5
5.5
6.5
7.5
8.5
9.5
pH OF GERMINATING MEDIUM

Self and Sib-Pollination: Six species including five dioecious types and one monoecious type were used in the determination of sib and self-compatibility. A total of 338 controlled sib- and self-pollinated flowers was involved in these studies. All the species selfed or sib-pollinated in this investigation set fruits which produced viable seed. Results of hand self and sib-pollination in relation to fruit set and seed germination are presented in Table V.

TABLE V

Fruit set by hand self and sib-pollination

Species (Index number)[a]	Number of flowers pollinated	Number of fruits set	Percent fruit set	Seed germination[b]
Female Male				
149♀ x 149♀	67	29	43.28	+++
125 x 125	53	50	94.34	+
145 x 145	50	44	88.00	+++
198 selfed	59	34	57.63	+++
195 x 195	43	20	46.41	++
131 x 131	66	57	86.36	+

[a] 149 .. .. C. goudotiana
125 .. .. C. pennata
145 .. .. C. cauliflora
198 .. .. C. monoica
195 .. .. C. goudotiana
131 .. .. C. parviflora

[b] Seed germination ratings
+++ .. .. Good
++ .. .. Fair
+ .. .. Poor
- .. .. No germination

Percentage fruit set was low for both forms of C. goudotiana (149 and 195) and C. monoica. However, seed germination was good for both C. goudotiana (149) and C. monoica but only fair for C. goudotiana (195). C. pennata and C. parviflora showed high percent fruit set but seed germination was markedly poor for both species. Fruit set and seed germination were high for C. cauliflora.

Cross-Pollination: Studies on cross-pollination were conducted on 1,859 flowers involved in 47 crosses and reciprocal crosses. Results indicated variability in the degree of cross-compatibility. Both cross-compatibility and cross-incompatibility were observed.

Results were broadly classified under four categories. Crosses which produced viable seed are recorded in Table VI. Except for the crosses, C. cauliflora (145) x C. monoica (198) and C. cauliflora (194) x C. pennata (125), fruit set was generally low. Crosses between C. goudotiana (149 and 195) and C. monoica produced markedly low percentage fruit set. Seed germination was also poor for these crosses even though seed from self- and sib-pollinations of these species showed fair to good viability. A cross between the two forms of C. cauliflora (145 and 194) yielded only 50% fruit set. Seed viability was also poor. Crosses between the two forms of C. goudotiana (149R and 149Y) also produced low fruit set but seed viability was good. When C. pennata (125) was crossed to both forms of C. cauliflora very different results were obtained. The cross C. cauliflora (194) x C. pennata produced 100% fruit set while in the cross C. cauliflora (145) x C. pennata only 41.67% fruit set was obtained. Seed germination was low in both

crosses. Crosses between the two forms of C. cauliflora and C. monoica produced fairly high fruit set as well as fair seed germination.

Table VII shows the crosses which, although set fruit, did not produce viable seed. Examination of the seeds showed that they were all empty. Many of the seeds were slightly smaller than normal. It was further observed that at the early stages of their development the immature seeds did have contents but during the process of maturation the contents were lost. The cause of this is not known. Whether these immature seeds could be grown by embryo culture technique needs to be investigated further. Crosses in Table VIII set seedless fruits. In these crosses, pollination stimulated fruit development but seed was never developed. Recorded in Table IX are the crosses which produced completely negative results.

Data in Table X were obtained from six reciprocal crosses. Reciprocal crosses were fewer than original crosses because in some of the species only the female plants were represented. It was therefore impossible to arrange crosses in which these species could be used as male parents. It can be seen that the reciprocal crosses did not produce similar results with respect to fruit set and seed viability. Used as a pollen parent C. monoica set fruit (with viable seed) fairly easily with C. cauliflora (145), C. goudotiana (149) and C. goudotiana (195). However, in reciprocal crosses viable seed was only obtained with C. cauliflora (145). Seed viability of the reciprocal cross C. monoica (198) x C. goudotiana (149R) was not tested because fruits had not matured at the time of writing. The reciprocal cross between C. monoica and C. goudotiana (195) failed to set viable seed. Similarly, when C. pennata

was used as a male parent it set fruit (with viable seed) easily with C. cauliflora. The reciprocal cross produced seed without viable embryos. Both original and reciprocal crosses between C. goudotiana (Red) and C. goudotiana (Yellow) were low in fruit set but seed germination was good.

TABLE VI

Fruit set by hand cross-pollination

Species (Index number)[a]			Number of flowers pollinated	Number of fruits set	Percent fruit set	Seed germination
Female		Male				
145	x	198	65	58	89.23	++
149	x	198	73	13	17.81	+
203	x	198	30	12	60.00	++
145	x	125	72	30	41.67	+
194	x	145	40	20	50.00	+
194	x	125	48	48	100.00	+
194	x	198	45	27	60.00	++
131	x	149R	58	26	44.82	+
195	x	198	55	15	27.27	+
149R	x	149Y	37	9	24.32	+++

[a]
145 .. .. C. cauliflora
198 .. .. C. monoica
149 .. .. C. goudotiana
203 .. .. C. species
125 .. .. C. pennata
194 .. .. C. cauliflora
131 .. .. C. parviflora
149R .. .. C. goudotiana (Red)
149Y .. .. C. goudotiana (Yellow)

TABLE VII

Miscellaneous crosses which set fruits producing non-viable seeds

Crosses (Index number)[a]			Number of flowers pollinated	Number of fruits set	Percent fruit set	Seed germination[b]
Female		Male				
125	x	198	42	16	38.10	-
145	x	149R A	50	41	82.00	-
A 149R	x	125	44	7	15.91	-
$26F_4$	x	145 A	38	24	63.16	-
$26F_4$	x	131	30	15	50.00	-
$26F_4$	x	198	45	12	26.67	-
$26F_4$	x	149R	36	24	66.67	-
145	x	131	61	53	86.89	-
194	x	$26F_4$	18	12	66.67	-
203	x	131	18	9	50.00	-
203	x	149R	24	12	50.00	-
203	x	195	18	12	66.67	-
198	x	131	28	8	28.56	-

[a]
198 .. .. C. monoica
149 .. .. C. goudotiana
125 .. .. C. pennata
145 .. .. C. cauliflora
$26F_4$ .. .. C. papaya
131 .. .. C. parviflora
194 .. .. C. cauliflora
203 .. .. C. species
195 .. .. C. goudotiana
149R .. .. C. goudotiana

[b] Seed germination rating

\- .. .. No germination

TABLE VIII

Miscellaneous crosses which produced seedless fruits

Cross (Index number)[a]	Number of flowers pollinated	Number of fruits set	Percent fruit set
Female Male			
125 x 195	24	12	50.00
$5BF_{12}$ x 125	36	10	27.78
149 x 145	58	18	31.04

[a] 125 .. .. C. pennata
195 .. .. C. goudotiana
$5BF_{12}$ .. .. C. papaya
149 .. .. C. goudotiana
145 .. .. C. cauliflora

TABLE IX

Crosses which failed to set fruits

Cross (Index number)[a]			Number of flowers pollinated	Number of fruits set	Percent fruit set
Female		Male			
125	x	149R	30	0	0.0
125	x	$5BF_{12}$	20	0	0.0
149R	x	$5BF_{12}$	35	0	0.0
198	x	$26F_4$	23	0	0.0
131	x	198	38	0	0.0
131	x	125	36	0	0.0
131	x	145	58	0	0.0
131	x	195	20	0	0.0
198	x	125	30	0	0.0
145	x	195	24	0	0.0
203	x	$26F_4$	18	0	0.0
203	x	125	29	0	0.0
$5BF_{12}$	x	131	16	0	0.0
$5BF_{12}$	x	198	35	0	0.0

[a]

125	..	..	C. pennata
149R	..	..	C. goudotiana
$5BF_{12}$	..	..	C. papaya
198	..	..	C. monoica
131	..	..	C. parviflora
145	..	..	C. cauliflora
195	..	..	C. goudotiana
203	..	..	C. species
$26F_4$	..	..	C. papaya

TABLE X

Fruit set and seed viability in six reciprocal crosses

Species (Index number)[a]			Number of flowers pollinated	Number of fruits set	Percent fruit set	Seed germination[b]
Female		Male				
198	x	145	60	24	40.00	++
145	x	198	65	58	89.23	++
149R	x	198	73	13	17.81	+
198	x	149R	40	8	20.00	not tested
125	x	145	66	30	45.45	-
145	x	125	72	30	41.67	+
149	x	131	80	19	23.75	-
131	x	149	58	26	44.82	+
198	x	195	20	4	20.00	-
195	x	198	45	27	60.00	++
149Y	x	149R	38	10	25.32	+++
149R	x	149Y	37	9	24.32	+++

[a]
198 .. .. C. monoica
145 .. .. C. cauliflora
149 .. .. C. goudotiana
125 .. .. C. pennata
131 .. .. C. parviflora
195 .. .. C. goudotiana
149Y .. .. C. goudotiana (Yellow)
149R .. .. C. goudotiana (Red)

[b] Seed germination ratings

+++ .. .. Good
++ .. .. Fair
+ .. .. Poor
- .. .. No germination

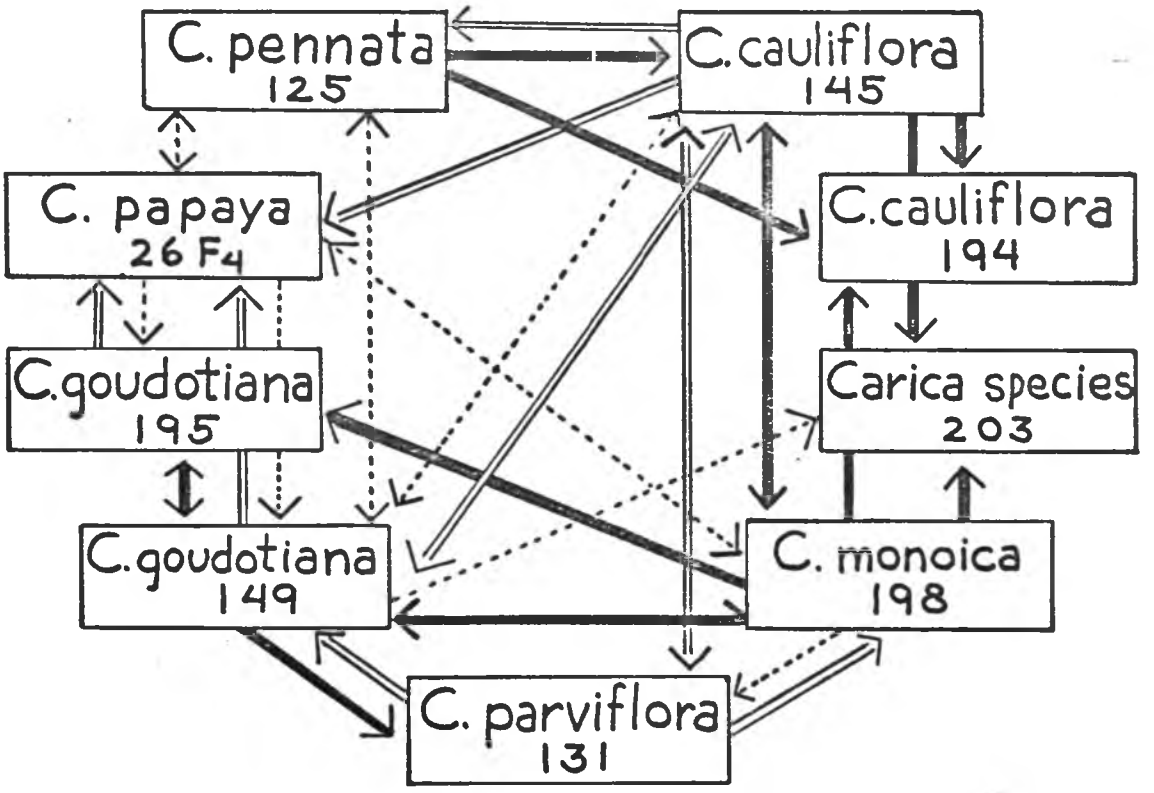
The results of cross-pollinations obtained here were in general agreement with cross compatibility results presented by Jimenez and Horovitz (1958). These authors conducted cross compatibility studies in six Carica species including three of those investigated in the present work. Jimenez and Horovitz found that some crosses set viable seed, some required embryo culture and others produced negative results. In the studies reported here, crosses between hermaphrodite plants of C. papaya L. and the male plants of C. cauliflora, C. goudotiana, C. parviflora and C. monoica (monoecious) sometimes produced undersize fruits. These fruits contained undersize seeds all of which were empty. Crosses between hermaphrodite plants of C. papaya and C. pennata yielded parthenocarpic fruits. Crosses between female plants of C. papaya and C. cauliflora (male) also set small seedless fruits. The reciprocals of these crosses using pollen from C. papaya produced negative results.

Two crosses which had never taken in previous studies, Warmke et al. (1957), Jimenez and Horovitz (1967) were successful in the present work after repeated attempts. These crosses were C. monoica x C. goudotiana and C. parviflora x C. goudotiana.

Results of pollen germination undertaken here showed that all the species produced viable pollen. The negative results obtained in some crosses were therefore likely due to inherent factors other than production of non-viable pollen. The fact that certain crosses such as the two mentioned above did set viable seed after repeated attempts, indicated that environmental influence may have been involved in the observed incompatibility. Hand pollinations were made all the year

round during the course of the experiment. It was observed that crosses made during the winter months when it was wet and cool produced higher percentage of fruit set than those of summer months when it was hot and dry. During the summer months production of female flowers slowed down and rate of flower drop was higher than in the winter months. It was very likely that water stress and high temperatures also contributed to the failure of crosses to set fruits. A diagrammatic scheme of cross compatibility of the species as observed in these studies is presented in Figure 3.

Figure 3: A diagrammatic scheme showing cross compatibility of some Carica species.



ARROW POINTS IN THE DIRECTION OF FEMALE PARENT

CROSS FERTILE

FRUIT SET BUT NO VIABLE SEED

NO FRUIT SET OBTAINED

SEED VIABILITY NOT TESTED

Description of F_1 Hybrid Plants: As a result of cross-compatibility studies conducted as part of the present investigation, nine interspecific and one intraspecific hybrids were produced. A general description of these hybrids based on observations and measurements taken under the conditions of the experiment is given below. All measurements were taken eight months after seedlings were field planted. The numerical values given for length of leaves, length of flower buds, fruit shape index and fruit weight were compiled on tree to tree basis. Each value therefore represents the mean of means ± S.E.

Carica goudotiana (149R) x C. monoica (198): These interspecific hybrids were very uniform. Average eight month tree height was 2.13±0.07 meters and trunk circumference (one foot above ground level) was 33.53±0.74 cm. Trees were profusely branched like C. monoica. Stem color was red but variations in color intensity were observed. Average leaf length was 81.58±1.33 cm. Leaf petioles and veins showed various shades of red. Leaves were five-lobed like C. goudotiana and each lobe was segmented into a number of secondary lobes.

Hybrid plants were monoecious like C. monoica. Male flowers were few in number relative to the number of female flowers produced. Flowers were produced only in the axils of young leaves, never on bare tree trunk. Flowers had a purple tinge like those of C. goudotiana. Male flowers averaged 2.60±0.03 cm. in length. Average length of female flowers was 2.51±0.02 cm. Hybrids were more productive than either of their parents. Number of fruits per peduncle ranged from one to seven. Fruit shape index was 1.45±0.02. Each fruit had five

ridges (carpel fusion lines) like those of C. goudotiana. Ripe fruit color was pink and average fruit weight was 135.68±5.43 grams.

C. goudotiana (195) x C. monoica (198): Index No. 195 is a form of C. goudotiana from Venezuela. Tree characteristics were generally similar to those of Index No. 149, but Index No. 195 produced only yellow fruits which were smaller in size and less elongated than those of Index No. 149.

Its hybrids with C. monoica were generally similar in appearance to those of Index No. 149 and C. monoica. Hybrids reached an average height of 2.20±0.08 meters in eight months and trunk circumference (one foot above ground level) averaged 34.54±1.29 cm. Trees were profusely branched. Stem color was green.

Leaves averaged 81.04±2.18 cm. in length. Leaf petioles and veins were red but there were variations in color intensity. There were five primary lobes and a number of secondary lobes to each leaf.

Hybrids were monoecious. Both male and female flowers were produced with about the same frequency. Male and female flowers had an average length of 2.37±0.07 cm. and 2.21±0.10 cm. respectively. Flowers had a purple tinge. Trees were very productive. Multiple fruiting was characteristic of the hybrids. Fruits had 'carpel fusion' ridges like those of C. goudotiana. Some of the hybrids produced fruits with yellow skin color while others produced orange colored fruits. Average fruit shape index was 1.25±0.02 and average fruit weight was 115.78±3.58 grams.

C. parviflora (131) x C. goudotiana (149R): Until now this cross had never been successful anywhere. In fact Horovitz & Jimenez (1967) cited the cross C. parviflora x Carica species as a general example of cross incompatibility in the family Caricaceae. In the present study it took about two and a half years of repeated attempts before the cross finally yielded a few viable seeds. F_1 plants were established and out of these, three are currently flowering. The numerical measurements given below were done on a single fruiting plant which was field planted. The others were planted in five-gallon cans in the Mid-Pac Nursery.

Vegetatively, these hybrid plants looked like their C. goudotiana parent. The height of plant was 1.91 meters after eight months. Tree trunk circumference was 24.5 cm. Stem color was variable ranging from light red to dark red. Average leaf length was 24.5 cm. The upper part of leaf lamina was dark green but the lower side sometimes showed a reddish blush. Leaf veins and petioles showed various shades of red. Leaves had five much segmented primary lobes.

Plants were dioecious. Flowers were dark pink like those of C. parviflora but were slightly bigger in size. Average female flower length was 2.20 cm. Between five and thirteen female flowers were produced per raceme and each could set fruit. Unripe fruit was green with five pink ridges (carpel fusion lines). On ripening, fruits turned purplish red. Fruits were small in size weighing on the average, 6.10 grams. Average fruit shape index was 2.80.

C. cauliflora (145) x C. monoica (198): These hybrids were very uniform. They attained an average height of 2.20±0.02 meters in eight months. Average trunk circumference (at the base) was 38.95±0.81 cm. Trees were profusely branched and some branches approached the main stem in size. Leaves averaged 102.51±1.46 cm. in length, five-lobed and dark green. There was no anthocyanin in petioles and veins.

Trees were monoecious and flowers were borne in axils of leaves and also on bare trunk. Immature flowers were green but became white at maturity. Length of male flowers was 3.71±0.04 cm. and female flowers averaged 3.39±0.04 cm. in length.

Flowers were borne on a much branched raceme, each branch of which terminated (usually) with a pistillate flower. Each pistillate flower was flanked by many staminate flowers on the same raceme. Occasionally a staminate flower was produced in a terminal position.

Tree productivity was significantly higher than that of either parent. Number of fruits set per raceme ranged from one to fourteen. Carpellodic fruits were fairly common. Fruits were green when immature, yellow when just ripe and orange when overripe. Each fruit showed carpel fusion lines represented by five wide and shallow grooves like those of C. monoica. Average fruit shape index was 1.77±0.01. Each fruit weighed 83.95±2.21 grams.

C. cauliflora (145) x C. pennata (125): Badillo (1967) had claimed that C. cauliflora and C. pennata were synonymous. Cross compatibility studies undertaken as part of this work showed that viable seed was obtained between the two plants only when C. cauliflora was used as a female parent. The two plants also differed considerably in fruit

shape and size as well as in raceme lengths. In view of these the two plants were regarded as two different species in this study.

The hybrids showed vigorous vegetative growth and attained an average height of 2.30±0.02 meters in eight months with an average trunk circumference (one foot from ground level) of 44.20±1.29 cm. Trees were seldom branched. Average length of leaves was 136±1.63 cm. Leaves had five primary lobes and each primary lobe was subdivided into a number of secondary lobes. Leaves were dark green but petioles and veins were light green or purplish in color. Trees were dioecious. Flowers were borne on racemose inflorescence in axils of leaves. Quite often flowers were also borne on bare tree trunk. Average length of male flowers was 3.87±0.12 cm. and that of female flowers was 3.76±0.06 cm. Flowers were green when immature but became white at maturity. Female plants were highly fertile. Fruits were intermediate in shape between those of both parents. Fruit shape index was 1.34±0.03. Fruits occurred either singly or in clusters of up to nine fruits per peduncle. Fruits were dark-green when unripe but yellow or orange when ripe. Each fruit was distinctly marked by five furrows (carpel fusion lines) running longitudinally from the anterior end to the posterior end of fruit. Average fruit weight was 124.32±10.71 grams.

C. cauliflora (194) x C. cauliflora (145): This was an intraspecific hybrid. Index Nos. 145 and 194 were obtained from Venezuela and El Salvador, respectively. The two looked alike vegetatively except that 194 was a bigger plant than 145. Fruits of 145 were slightly longer than those of 194.

The hybrids were very uniform and were much bigger plants than either parent. They attained an average height of 2.27±0.07 meters eight months after field planted. Eight month girth averaged 40.64± 1.08 cm. Trees were seldom branched. Average leaf length was 127.41± 2.46 cm. Leaves were five-lobed, dark green and sometimes had anthocyanin in veins and petioles.

Trees were dioecious. Flowers were borne either in leaf axils or on bare tree trunk, a characteristic also exhibited by both parents. Male flower length was 3.71±0.08 cm. Female flower length was 3.55± 0.13 cm. Flowers were green when immature but white at maturity.

Female plants were highly fruitful. Fruits were generally longer than those of either parent. Average fruit shape index was 1.77±0.06. The number of fruits per peduncle ranged from one to eight. Each fruit was marked by five narrow grooves (carpel fusion lines). Fruits were green when unripe but yellow or orange when ripe. Average single fruit weight was 121.81±10.51 grams.

C. cauliflora (194) x C. pennata (125): Index No. 194 was another form of C. cauliflora introduced from Venezuela. It was a bigger tree than Index No. 145 which was introduced from El Salvador. Index No. 194 also produced fruits which were not as elongated as those of Index No. 145.

Its hybrids with C. pennata were vigorous and reached an average height of 2.39±0.08 meters in eight months. Average trunk circumference was 46.07±1.40 cm. Trees were seldom branched. Average leaf length was 124.60±2.60 cm. Leaves were five-lobed and dark green but

leaf petioles and veins showed various shades of purple.

Trees were dioecious. Flowers were borne in axils of young leaves and on bare trunk just above old leaf scars. Average length of male flowers was 4.50±0.19 cm. Female flowers reached an average of 3.87± 0.15 cm. in length. Flowers were light green when immature but became progressively lighter in color and at anthesis they were white.

Fruiting was heavy and number of fruits per peduncle ranged from one to five. Fruits were intermediate in shape between those of both parents. Fruit shape index was 1.26±0.06. Fruits were yellow or orange when ripe and each had five narrow grooves (carpel fusion lines). Average fruit weight was 98.16±12.91 grams.

C. species (203) x C. monoica (198): These hybrids attained an average height of 1.72±0.08 meters in eight months. Trunk circumference was 20.74±2.49 cm. Trees were freely branched like C. monoica. Leaves averaged 58.00±0.23 cm. in length. Lobation of leaves was mixed. Leaves were mostly five-lobed but some were three-lobed. Leaves were green except for petioles and veins which were purplish.

Trees were monoecious. Flowers were produced in axils of young leaves. Flowers were green when immature but became pale yellow at maturity.

Trees were extremely fertile. Fruits occurred either singly or in clusters of up to twelve per peduncle. Fruits were intermediate in shape between those of both parents. Fruit shape index was 1.06±0.02. Ripe fruits were yellow or orange in color. Each fruit had five grooves which were wide and shallow. Fruits were small in size each weighing 30.07±2.38 grams.

C. cauliflora (194) x C. monoica (198): These hybrids were very big and vigorous and reached an average height of 2.47±0.05 meters in eight months. Average trunk circumference was 44.78±1.07 cm. Trees were freely branched but there was a distinct main trunk. Average leaf length was 95.88±1.14 cm. Leaves were five-lobed. Leaf lamina was dark green but leaf petioles and veins were either light green or purplish.

Plants were monoecious like C. monoica. Flowers were produced both at the axils of young leaves and on bare tree trunk. Mean length of male flowers was 3.46±0.08 cm. Mean length of female flowers was 2.80±0.12 cm. Immature flowers were green but became white at maturity. Fruiting was very heavy. Fruits sometimes occurred singly but in most cases, in clusters up to twelve fruits per peduncle. Fruits were intermediate in shape between those of both parents. Mean fruit shape index was 1.36±0.06. Fruits were yellow or orange when ripe and each fruit had five wide and shallow grooves (carpel fusion lines) similar to those of C. monoica. Average fruit weight was 139.47±13.81 grams.

Index No. (203) x C. cauliflora (145): Index No. 203 was a female of an unidentified species from Colombia. These interspecific hybrids reached an average height of 1.75±0.04 meters in eight months. Tree trunk circumference averaged 27.23±0.72 cm. in eight months under field conditions. Trees branched late during vegetative growth. Branches were few and confined to the lower half of plant. Leaves had five primary lobes and a number of secondary lobes. Leaf lamina was green but petioles and veins contained some purple pigment. Average leaf length was 80.05±0.44 cm.

Trees were dioecious and female flowers were borne only at the axils of young leaves but male flowers occurred both in leaf axils and on tree trunks. Immature flowers were dark green but at maturity became whitish at the tips and pale green below. Male flowers were 3.24±0.04 cm. in length and female flowers averaged 2.97±0.03 cm. in length.

Fruiting was heavy and fruits were borne either singly or in clusters of up to fifteen fruits per peduncle. Fruits were intermediate in shape between those of the parents. Fruit shape index was 1.18±0.03. Ripe fruit color was either yellow or orange. Average fruit weight was 57.00±3.16 grams.

All the interspecific hybrids developed in the present work were found to be very uniform and vegetatively more vigorous and more fruitful than their parents.

C. monoica showed the ability to retain its fruits for a long period of time. Fruits of C. monoica which were tagged when they had just begun to ripen remained attached to the plant for periods ranging from nine months to over twelve months except when damaged by storm or lost through disease. The fruits remained firm all throughout the life span of the plant. A similar experiment conducted for C. cauliflora and C. goudotiana showed that the former took only an average of 2.4 weeks from beginning of ripening to fruit drop and the latter took 5.3 weeks. The fruits of the hybrids, C. cauliflora x C. monoica and C. goudotiana x C. monoica, in the absence of a storm or disease, took over a year from beginning of ripening to fruit drop. The ripe fruits remained relatively firm and in many cases germination of seeds occurred within the fruits while the latter were still attached to the parent

plants.

A number of Carica species including C. cauliflora have been reported to be resistant to some virus diseases (Horovitz and Jimenez, 1967). These authors also reported that crosses between resistant and susceptible species produced resistant F_1 hybrids. In the present work no disease innoculations were made to determine the presence or lack of resistance. However, during the course of the experiment there was an outbreak of a virus disease in the field in which species and species hybrids were growing. The incidence of the disease was near an epidemic level. It was observed that only C. cauliflora and the F_1 hybrids which had C. cauliflora as one of their parents did not show any symptoms of the disease. It was rather interesting to find that none of the other species and F_1 hybrids that were susceptible died as a result of the attack. All the C. papaya plants that were planted in the same field died from the attack. The other species although showed the symptoms of infection both in the leaves and on the fruits were able to tolerate the disease. All species and hybrids were found susceptible to mite attack. Loss of plants was mostly due to root rot. Root rot disease was not observed for C. cauliflora or any of its hybrids with C. monoica, a species susceptible to root rot (personal observation).

PLATE I: General morphology and growth habits of two *Carica* species and their interspecific hybrid.

Figures:

4. *C. goudotiana* (male)
5. *C. goudotiana* (female)
6. *C. monoica* (monoecious)
7. *C. goudotiana* x *C. monoica* (monoecious).

I

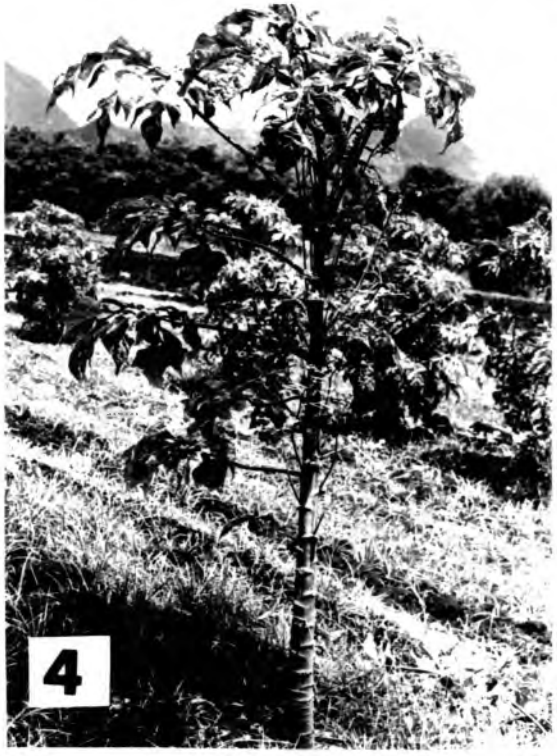


PLATE II: General morphology and growth habits of Carica parviflora and those of its hybrid with C. goudotiana.

Figures:

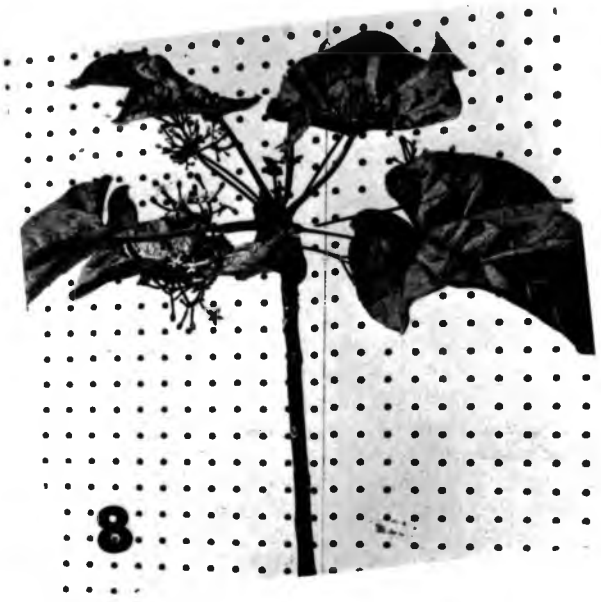
8. C. parviflora (male)

9. C. parviflora (female)

10. C. parviflora x C. goudotiana (male)
(compare Figs. 4 and 5)

11. C. parviflora x C. goudotiana (female)
(compare Figs. 4 and 5)

II


8


9


10


11

PLATE III: General morphology and growth habits of two *Carica* species and their interspecific hybrid.

Figures:

12. *C. cauliflora* (male)
13. *C. cauliflora* (female)
14. *C. cauliflora* x *C. monoica* (monoecious)

III

PLATE IV: General morphology and growth habit of *Carica pennata* and those of its hybrid with *C. cauliflora*.

Figures:

15. *C. pennata* (male) (compare Fig. 12 for length of raceme)

16. *C. pennata* (female) (compare Fig. 13 for shape of fruits)

17. *C. cauliflora* x *C. pennata* (male)

18. *C. cauliflora* x *C. pennata* (female)


15


16


17


18

PLATE V: General morphology, growth habits and fruits of some Carica species and hybrids.

Figures:

19. C. cauliflora 194 x C. cauliflora 145 (female) (intraspecific hybrid)

20. C. cauliflora 194 x C. pennata (female) (interspecific hybrid)

21. Fruits of C. cauliflora 145 (A), C. pennata (B) and C. cauliflora 145 x C. pennata (A x B) Note shapes of fruits. (Scale in inches)

V

19

20

A A × B B

21

PLATE VI: General morphology of some Carica interspecific hybrids.

Figures:

22. Carica species 203 x C. monoica (monoecious) (branches removed)

23. C. cauliflora 194 x C. monoica (monoecious) (branches removed)

24. Carica species 203 x C. cauliflora 145 (male)

25. Carica species 203 x C. cauliflora 145 (female)


22


23


24


25

Heterosis: Heterosis has been defined either as the average excess in vigor which F_1 hybrids exhibit over the midpoint between the means of the inbred parental lines or as the average excess in vigor which F_1 hybrids exhibit over the mean of the better parental line. On the basis of the characters studied in this investigation it made more sense to make comparisons between the means of the hybrids and those of their better parental lines. In terms of the vegetative and the productivity characters used here in the assessment of heterotic effects, both C. cauliflora and C. goudotiana were found superior to C. monoica, see Table XI.

TABLE XI

The means and standard errors of parental lines and F_1 hybrids with respect to tree height, trunk circumference, total number of fruits and total weight of fruits

Plant	Character measured ($\bar{X} \pm$ S.E.)			
	Tree height (meters)	Trunk circumference (cm)	Total number of fruits	Total weight of fruits (kilograms)
C. monoica (parent)	1.47±0.04	16.51±0.73	121.00±17.33	6.55±1.09
C. cauliflora (parent)	1.90±0.01	32.88±0.45	189.81±3.17	18.17±0.54
C. goudotiana (parent)	1.96±0.10	29.21±0.87	140.70±8.60	26.53±2.39
C. cauliflora x C. monoica (hybrid)	2.20±0.02	38.95±0.81	425.05±10.22	35.60±1.21
C. goudotiana x C. monoica (hybrid)	2.13±0.07	33.53±0.74	347.80±35.75	47.10±5.16

Accordingly, in all characters measured, comparisons were made between the means of C. cauliflora and those of the hybrid, C. cauliflora x C. monoica. Similar comparisons were made between C. goudotiana and the hybrid, C. goudotiana x C. monoica.

Observed differences in eight month tree height, eight month trunk circumference, total number of fruits and total weight of fruits between C. cauliflora and C. cauliflora x C. monoica are given in Table XII. Analysis was done using the F-test. Error variance is that within generations.

Highly significant differences between the superior parental line and the F_1 hybrids were found in all four characters. This seems to indicate that the F_1 hybrids exhibited pronounced heterotic effects in terms of vegetative vigor as well as productivity.

Results of similar comparisons made between C. goudotiana and F_1 hybrid, C. goudotiana x C. monoica are presented in Table XIII.

In this single cross no significant differences in eight month tree height were obtained between the goudotiana parent and the F_1 hybrid. However, highly significant differences were observed in trunk circumference, total number of fruits and total weight of fruits.

It is worthy of mention that although the two interspecific hybrids showed significant superiority over their better parents in total weight of fruits produced, average single fruit weight was in favor of both parents. The average single fruit weight of C. goudotiana was 186.30±9.57 grams (mean ± S.E.) as compared to that of its hybrid with C. monoica which was 135.68±5.43 grams. Similarly the average single fruit weight of C. cauliflora was 95.03±2.23 grams

(mean ± S.E.) while that of its hybrid with C. monoica was 83.95±2.21 grams. It was therefore the high productivity exhibited by the hybrids in total number of fruits set that was accountable for the total fruit weight advantage they showed over their better parents. The observed individual fruit weight reduction was probably due to the increase in number of fruits per tree. It must be emphasized however that the comparison made here strictly involved hybrids versus the high parents. If the comparison had been made between the hybrid mean and the mid-parental value, which is also a valid way of estimating heterosis, average single fruit weight would be in favor of the hybrids. In terms of average single fruit weight, the mid-parental value of C. cauliflora and C. monoica was 74.30 grams as compared to that of their hybrid which was 83.93 grams. Similarly, the mid-parental value in terms of average single fruit weight of C. goudotiana and C. monoica, was 119.93 grams while the average fruit weight of their hybrid was 135.68 grams.

These results proved rather conclusively that these members of the genus, Carica do exhibit heterosis both with respect to vegetative and productivity characters. The F_1 hybrids were not only taller and more robust than either parent but they also significantly out yielded both parents in terms of total number of fruits produced and in total weight of fruits.

Hybrid vigor (heterosis) has been conclusively demonstrated for a number of plant species including Zea mays, Medicago sativa, Brassica oleracea capitata, Arachis hypogeae, Nicotiana tabacum, Gossypium arboreum, Ricicus communis L., and a host of other species. Its prescence, however, has not yet been conclusively established in the genus,

Carica. Several workers including Hofmyer (1941), Hamilton (1954), and Nakasone and Storey (1955) did not detect any evidence of hybrid vigor in progenies of crosses involving inbred lines of C. papaya L. It must be mentioned that Traub et al. (1942) did mention that a cross between two inbred lines of C. papaya L., Orlando x Fairchild, gave more vigorous progeny than that from selfed parents. No data were presented to substantitate this claim. All the authors mentioned above worked with C. papaya L., the only species of commercial significance in the genus, Carica. Investigation was mostly limited to vegetative vigor and no yield comparisons were reported. Inbreds were either those of varieties of the same species or strains of the same cultivar.

It has been shown (cf. Allard, 1960) that hybrids between inbreds of diverse parentage generally give greater hybrid vigor than hybrids between inbreds derived from the same or similar varieties. It is highly probable that one of the reasons for failure of several workers to detect heterosis in previous investigations was that the inbreds crossed were very closely related and had many genes in common.

TABLE XII

Analysis of variance of tree height, trunk circumference, number of fruits and total fruit weight for *Carica cauliflora* and *C. cauliflora* x *C. monoica*

Character	Source of variation	D.F.	S.S.	Variance	F value
Eight month tree height	Total	41	1.32	-	
	Between generations	1	0.94	0.94	98.95 **
	Within generations (Error)	40	0.38	0.0075	
Eight month trunk circumference	Total	41	748.07	-	
	Between generations	1	386.81	386.81	42.84 **
	Within generations (Error)	40	361.25	9.03	
Total number of fruits	Total	41	628706.29	-	
	Between generations	1	581038.10	581038.10	487.57 **
	Within generations (Error)	40	47668.19	1191.70	
Total fruit weight	Total	41	3965.65	-	
	Between generations	1	3226.13	3226.13	174.48 **
	Within generations (Error)	40	739.52	18.49	

** Significant at the 1% level

TABLE XIII

Analysis of variance of tree height, trunk circumference, number of fruits and total fruit weight for *Carica goudotiana* and *C. goudotiana* x *C. monoica*

Character	Source of variation	D.F.	S.S.	Variance	F value
	Total	19	1.53	-	
Eight month tree height	Between generations	1	0.14	0.14	1.75
	Within generations (Error)	18	0.39	0.08	
	Total	19	210.00	-	
Eight month trunk circumference	Between generations	1	93.23	93.23	14.37 **
	Within generations (Error)	18	116.77	6.48	
	Total	19	335949.75	-	
Total number of fruits (first crop)	Between generations	1	214452.05	214452.05	31.77 **
	Within generations (Error)	18	121497.70	6749.87	
	Total	19	5064.57	-	
Total fruit weight (first crop)	Between generations	1	2115.63	2115.63	12.91 **
	Within generations (Error)	18	2948.94	163.83	

** Significant at the 1% level

It is of interest to note that after the third time of sib-mating, the progenies of C. goudotiana showed considerable reduction in size and in total number of fruits produced. Differences were also observed in tree height and stem circumference, the F_3 trees being shorter and less vigorous than F_2 plants, see Table XIV. All measurements, counts and weights were taken eight months after seedlings had been field planted.

TABLE XIV

Differences (mean ± S.E.) observed in vegetative and productivity characters between F_2 and F_3 sib-mated progenies of C. goudotiana

Generation	Tree height (meters)	Trunk circumference (cm.)	Total number of fruits set	Single fruit weight (gm.)	Total fruit weight (Kilos)
F_2	1.96±0.10	29.21±0.87	140.70±8.60	186.30±9.57	26.53±2.39
F_3	1.58±0.06	21.26±0.88	64.1±6.30	112.44±8.13	7.24±0.92

A decline was also observed in C. monoica after selfing it for the third time. This was most noticeable in seedling mortality rate which rose from 30% in the F_2 generation to 72% in the F_3 generation. However, those which survived did not show any decline in vigor relative to those of the preceding generation.

Seedlings of the third generation of C. cauliflora were not field planted and their field performance could not be assessed. However, a drop was observed in seed germination rate which fell from 58% in the second generation to 52% in the third generation.

It was difficult to say whether the depression in field performance observed in C. goudotiana and C. monoica was a result of inbreeding or a consequence of the 'replant problem'. The F_3 seedlings were planted on a piece of land which had been used in growing C. papaya and other Carica species for two consecutive periods. Although the soil was pre-treated with captan (40 lbs. per acre) before the third planting, there was no assurance that the treatment was entirely effective. F_2 seedlings were planted on a semi-virgin land which had not been used for papaya cultivation for several years. These seedlings were therefore not predisposed to poor performance as the F_3 seedlings. It may be mentioned here also that the hybrid seedlings of C. cauliflora and C. monoica which were planted on the same piece of land as the F_3 seedlings of C. goudotiana and C. monoica did not suffer any noticeable setback.

Inbreeding, like heterosis is a controversial issue as far as papaya breeding is concerned. Deterioration of populations subjected to continued consanguineous mating has been observed in several plant species. In the present studies the circumstances of the experiment did not justify any categorical statement with regard to the presence or absence of inbreeding. For dioecious species such as most of those investigated here, sib-mating was the closest form of inbreeding possible. The decline observed in general vigor (tree height, trunk circumference), increased rate of mortality and reduction in yield in F_3 plants were in keeping with the deterioration which usually resulted from inbreeding. However, the intervention of the 'replant problem' referred to above made it impossible to separate any probable adverse effects of inbreeding from the setbacks which usually manifest

themselves in replant fields. The fact that second generation progenies were grown on a semi-virgin land while the third generation seedlings were established in a replant field made a fair comparison of both generations impossible. However, it is most likely that the 'replant problem' was a more important factor in the deteriorations observed than the loss of vigor due to inbreeding. This is rendered more probable by the fact that a few seedlings of the F_3 generation which were planted in five-gallon cans in an artificial medium (sterilized soil, sponge-rok, peat moss), did not show any noticeable loss of vigor comparable to that observed among field planted seedlings. These species had been perpetuated throughout the years by sib-pollinations. If the adverse effects of inbreeding were very pronounced, by now these species would have become extinct. It is suggested that in later work along this line seedlings of the generations to be compared should be handled under the same conditions.

INHERITANCE STUDIES

Stem Color: With reference to stem color the species studied fell into two categories: red and green. The species which had red stems were the two forms of C. goudotiana (149R and 195), and Index No. 203. Species which had green stems included C. pennata (125), C. cauliflora (145), C. monoica (198), C. parviflora (131) and C. goudotiana (149Y). A preliminary experiment involving two interspecific crosses and three sib-matings showed that crosses among red-stemmed plants produced only red-stemmed plants while crosses among green-stemmed plants produced only green-stemmed plants (Table XV). The progenies of the sib-pollinations were scored at the seedling stage because a large number of these could not be field planted. The results indicated that green-stemmed plants bred true for green-colored stem and red-stemmed plants bred true for red stem color.

Three interspecific and one intraspecific crosses were made between red-stemmed and green-stemmed parents. Results of these crosses showing the stem color of their F_1 hybrids as well as their F_2 and backcross progenies are presented in Table XVI. Similar segregation ratios were obtained in all the crosses. The results were therefore pooled for analysis. Chi-square values for both F_2 and backcross progenies are presented in Table XVII. Differences in intensity of the red stem color were observed in the F_1, F_2 and backcross progenies. The intensity of the red ranged from dark red through red to light red. An attempt to determine the mode of inheritance for these color variations did not reveal any definite pattern, probably because of

difficulty in scoring for shades of stem color. In determining genetic ratios the red-stemmed plants of all shades were grouped together under one class as red.

TABLE XV

Stem color of progenies of crosses and sib-matings among green-stemmed and red-stemmed parents

Parents	F_1 Stem color	F_2 progenies		Backcross P_1		Backcross P_2	
		Red	Green	Red	Green	Red	Green
Female P_1 Male P_2							
149R Red x 149R Red	Red	70	0	-	-	-	-
195 Red x 195 Red	Red	55	0	-	-	-	-
149Y Green x 149Y Green	Green	0	60	-	-	-	-
198 selfed Green	Green	0	38	-	-	-	-
145 Green x 198 Green	Green	0	96	0	116	0	76
145 Green x 125 Green	Green	0	110	-	-	0	50

TABLE XVI

Stem color of progenies of interspecific and intraspecific crosses between red-stemmed and green-stemmed parents

Parents			F_1 Stem color	F_2 progenies		Backcross P_1		Backcross P_2	
				Red	Green	Red	Green	Red	Green
Female P_1		Male P_2							
149R	x	149Y				78 ~~40~~	0 ~~36~~	40 ~~78~~	36 ~~0~~
Red		Green	Red	202	62				
195	x	198							
Red		Green	Red	78	27	-	-	-	-
203	x	198							
Red		Green	Red	53	21	~~26~~	~~30~~	26	30
149R	x	198				65 ~~50~~	0 ~~58~~	50 ~~65~~	58 ~~0~~
Red		Green	Red	190	75				
		TOTAL		523	185	~~116~~ 143	~~124~~ 0	~~143~~ 116	~~0~~ 124

TABLE XVII

Chi-squares for stem color of F_2 and backcross progenies

Progeny	Observed		Calculated		Approximate ratio observed		Chi-square
	# Red	# Green	# Red	# Green	Red	Green	
F_2	523	185	531	177	3	1	0.48
BC_1	116	124	120	120	1	1	0.27
BC_2	143	0	143	0	1	0	0.00

It can be seen that crosses between red-stemmed and green-stemmed parents produced only red-stemmed F_1 plants. The F_2 progenies segregated into red-stemmed and green-stemmed plants in a ratio of 3 red : 1 green. Backcrosses of F_1 plants to their red-stemmed parents produced only red-stemmed plants while backcrosses of F_1 plants to their green-stemmed parents produced both red-stemmed and green-stemmed plants in a ratio of 1 red : 1 green. The results seem to indicate that stem color in the species under investigation is controlled by a single pair of genes with dominance for red stems and recessiveness for green stems.

Results like these showing a monogenic mode of inheritance for stem color with red stem color dominant to green stem color have been reported for other species including several species of Desmodium by Hutton and Gray (1967), Park and Rotar (1968) and Rotar and Kuan-Hon Chow (1971). In C. papaya Hofmyer (1938) also found that purple stem color was dominant to green stem color. These authors also found

differences in intensity of the red stem color.

The reason for variations in the intensity of the red stem color was not apparent. It is possible that modifier genes and intensifying genes are also involved in the determination of stem color in the species studied. No evidence of complementary gene action was detected in these studies.

Petiole Color: On the basis of petiole color the species studied could be classified into two categories: red and green. Crosses among species or varieties with red-colored petioles produced only plants with red petioles, while crosses among parents with green petioles produced plants with only green petioles.

Three crosses between parents with both types of petiole color were used to study the mode of inheritance of petiole color. The results of these crosses are presented in Table XVIII. All the F_1 hybrids were found to produce red-colored petioles. F_2 and backcross progenies segregated into red and green types. Backcross to red parents produced only red-petioled types. Backcrosses to the green parents also produced both red and green types. Variations in intensity of red were observed in the F_1 hybrids, F_2 generations and backcross progenies. It was observed that all red-stemmed plants also produced red petioles. However, there were some green-stemmed plants which also produced red-colored petioles.

To fascilitate classification, all red-petioled plants irrespective of their shades were grouped together as red. Since the results of all the three crosses were similar, the data were combined for presentation.

Out of a total of 424 plants scored for petiole color in the F_2 generation, 309 produced red-colored petioles and 115 had green petioles. These results were not significantly different from a ratio of 3 red : 1 green. The chi-square value was 1.89 and had a probability of between 0.250 and 0.100. A total of 331 plants were scored for petiole color in backcross (to the green parents) progenies. Out of these, 158 plants produced red-colored petioles and 173 produced green petioles. This segregation pattern approximated a 1 : 1 ratio. The chi-square value was 0.68 and had a probability of between 0.500 and 0.250.

These results seem to indicate a monogenic mode of inheritance for petiole color with dominance for red petiole color and recessiveness for green petiole color. The observed variations in intensity of red is probably suggestive of the presence of modifier genes in addition to the one major gene pair controlling the presence or absence of red (anthocyanin) in the petioles. The fact that both red-stemmed and green-stemmed plants did produce red-colored petioles seems to suggest that the modifier genes which are involved in the distribution of anthocyanin in the stems are different from those controlling the distribution of red color in the petiole. Additional information concerning the modifier genes could probably be obtained from quantitative and qualitative measurements of anthocyanin in petioles.

These results are in accord with those obtained by Hofmyer (1938) in his study of inheritance of purple color in C. papaya. Purple petiole color was found dominant to green petiole color. Segregation ratios indicated a monogenic mode of inheritance. Hofmyer suggested further studies to determine the basis of the differences observed in

the intensity of the purple. Angell and Gabelman (1970) also reached similar conclusions in their study of inheritance of purple petiole in carrot. These authors also established a monogenic inheritance with purple petiole color dominant to green petiole color. Variations in intensity of purple were also observed in both F_1 and F_2 plants. These were attributed to the probable action of modifier genes, see Table XIX.

TABLE XVIII

Petiole color of F_1 hybrids, F_2 and backcross progenies of three crosses between red-petioled and green-petioled parents

Cross (Index number)[a]		F_1 petiole color	F_2 generation		Backcross (to green)	
			Red	Green	Red	Green
Female	Male					
195 x (Red)	198 (Green)	Red	78	27	32	29
203 x (Red)	198 (Green)	Red	91	32	27	33
149R x (Red)	198 (Green)	Red	140	56	99	111
	Total		309	115	158	173

[a] 195 .. .. C. goudotiana
149R .. .. C. goudotiana
203 .. .. C. species
198 .. .. C. monoica

TABLE XIX

Chi-squares for petiole color of F_2 and backcross progenies

Progeny	Observed		Calculated		Chi-square
	Red	Green	Red	Green	
F_2	309	115	318	106	1.89
Backcross	158	173	165.5	165.5	0.68

Inheritance of Flower Color: Four different types of flower color were observed among the species studied. C. parviflora (131) produced pink flowers. All the progenies of this species raised by sib-mating produced only pink flowers. This was an indication that the species bred true with respect to pink flower color. C. goudotiana (149 and 195) produced flowers which had a purple strip on a greenish background. This color is referred to here as 'purple-blush'. Results of preliminary sib-pollinations among members of these species also showed that they bred true for flower color. A pale yellow color characterized flowers of C. monoica (198). Three generations of selfing this species produced progenies with only pale yellow flowers. Finally, the two forms of C. cauliflora (145 and 194) and C. pennata produced white flowers. Sib-pollinations and cross-pollinations among white flowered plants also showed that white flower color bred true.

In studying the mode of inheritance of flower color, three successful interspecific crosses were used. These were C. cauliflora (145) (white) x C. monoica (198) (pale yellow); C. goudotiana (149R) (purple-

blush) x C. monoica (198) (pale yellow); and C. parviflora (131) (pink) x C. goudotiana (149R) (purple-blush). In the cross between C. cauliflora (white) and C. monoica (pale yellow), all F_1 plants produced only white flowers. From a total of 95 F_2 plants, 70 produced white flowers similar to those of C. cauliflora and 25 produced pale yellow flowers like those of C. monoica. A chi-square value of 0.09 with a probability between 0.900 and 0.750 indicated a close approximation to the 3 : 1 ratio. A backcross of the F_1 to the white parent (93 plants) produced only white flowered plants. A backcross of the F_1 plants to the pale yellow parent produced 26 white flowered plants and 28 pale yellow. This segregation fitted a 1 : 1 ratio as expected. The chi-square value was 0.07 and had a probability between 0.900 and 0.750. These results indicate a monogenic mode of inheritance with white flower color dominant to pale yellow flower color. Hofmyer (1938) also found that white and yellow flower colors of C. papaya were under the control of one pair of genes. However, his results showed that yellow flower color was dominant to white flower color.

In C. goudotiana (purple-blush) x C. monoica (pale yellow) cross, all the F_1 plants produced purple-blush flowers. Out of a total of 82 F_2 plants, 56 produced purple-blush flowers and 26 produced pale yellow flowers. The chi-square value calculated on the basis of an expected 3 : 1 ratio was 1.97, a close fit to this theoretical ratio, its probability lying between 0.250 and 0.100. A backcross of the F_1 to the purple-blush parent yielded plants which produced only purple-blush flowers. A backcross of the F_1 to the pale yellow parent produced 32 purple-blush and 39 pale yellow. This was not significantly different

from an expected 1 : 1 ratio. The chi-square value was 0.69 with a probability between 0.500 and 0.250. These results also indicate a monogenic inheritance with dominance for purple-blush flower color and recessiveness for pale yellow flower color.

In the third cross, C. parviflora (pink) x C. goudotiana (purple-blush), only three of the F_1 plants had just begun to flower. Flowers were all pink. This is indicative of pink flower color being dominant to purple-blush. However, the mode of inheritance could not be determined because F_2 and backcrosses had not yet matured.

It might be mentioned here that crosses involving other color combinations could not be made because of cross incompatibility.

TABLE XX

Segregation of white and pale yellow flower colors in a cross between two species of Carica

C. candiflora (white) x C. monoica (yellow)

Cross/generation	Flower color segregation		Ratio observed		Chi-square
	# white	# pale yellow	white	pale yellow	
White x pale yellow .....(F_1)	63	0	1	0	
F_1 white selfed .....(F_2)	70	25	3	1	0.09
F_1 white x white(P_1) .....BC_1	93	0	1	0	0.00
F_1 white x pale yellow ....BC_2	26	28	1	1	0.47

TABLE XXI

Segregation of purple-blush and pale yellow flower colors in a cross between two species of Carica

Cross/generation	Flower color segregation		Ratio observed		Chi-square
	# purple blush	# pale yellow	purple blush	pale yellow	
Purple-blush x pale yellow .....F_1	24	0	1	1	
F_1 purple-blush selfed .....F_2	56	26	3	1	1.97
F_1 purple-blush x purple-blush..BC_1	111	0	1	0	0.00
F_1 purple-blush x pale yellow...BC_2	32	39	1	1	0.69

Although Hofmyer (1938) found that the yellow flower color was dominant to white in C. papaya L., other authors working with other plant species have found white dominant to some other colors. In carnation, Dianthus caryophyllus, Mehlquist (1939) found that white flower color was dominant to both yellow and cream. Davis et al. (1958) found that the white flower color of Impatiens balsamina L. was dominant to cream. Brewbaker (1962) also found that the white color of the corolla in white clover was dominant to cyanidin-red. All these authors, except Brewbaker, established a monogenic mode of inheritance in all the color traits investigated.

Results obtained in the study of the inheritance of purple-blush and pale yellow are not uncommon in the plant kingdom. Odland (1960) found that purple color of anthers in the genus Capsicum was dominant

to yellow. Park and Rotar (1968) also found that purple flower color was dominant to near white in Desmodium. These authors observed segregation ratios which indicated the involvement of a single gene pair between purple and yellow or near white. Similarly, Kamemoto and Storey (1955) observed that purple color of the flowers of the zig-zag plant Asystasia gangetica was dominant to yellow flower color, but their results indicated a trigenic mode of inheritance.

Inheritance of Ripe Fruit Skin Color: The two forms of C. goudotiana were used to determine the mode of inheritance of skin color of ripe fruit. One of the forms (149R) produced red fruits and the other (149Y) produced yellow fruits. Since plants were strictly dioecious, an indirect method was used because the phenotype of the male plant with respect to fruit color was unknown.

One male plant, hereby referred to as the 'Unknown', was chosen as the source of pollen and crossed to the female plants of both color variants. A cross between the red female and the 'Unknown' produced 38 female plants and the cross between the yellow female and the same 'Unknown' yielded 44 female plants. The results of the two crosses are shown in Table XXII.

TABLE XXII

Segregation ratios of red and yellow ripe fruit colors in crosses involving varieties of C. goudotiana

Cross	F_1 fruit color		Ratio observed		Chi-square
	# Red	# Yellow	Red	Yellow	
Red female x Unknown	31	7	3	1	0.88
Yellow female x Unknown	19	25	1	1	0.82

These results were explained on the basis of simple Mendelian genetics. It was assumed that the dominant gene, R was responsible for red fruit color and its recessive allele, r, for yellow fruit color. Since R is dominant to r the genotypes RR and Rr would be phenotypically identical both producing red fruits. The genotype of the yellow-fruited plant would be rr. The first cross (red female x Unknown) produced some yellow-fruited plants. This indicated that the red female contained the recessive gene r under a heterozygous condition. Its genotype must therefore be Rr. The ratio of red to yellow was 3 : 1. This meant that the genotype of the Unknown male was Rr. This was confirmed by the fact that in the second cross (Yellow female x Unknown) red-fruited plants and yellow-fruited plants appeared in a ratio of 1 : 1. The above crosses would therefore be as follows:

Cross 1	Red female x Unknown (Rr) (Rr)	
F_1	1 RR : 2 Rr : 1 rr (red) (red) (yellow)	
Ratio	3 red : 1 yellow	
Cross 2	Yellow female x Unknown (rr) (Rr)	
F_1	1 Rr : 1 rr (red) (yellow)	
Ratio	1 red : 1 yellow	

From these results it seemed that red ripe fruit color and yellow ripe fruit color are governed by one gene pair with red fruit color being dominant to yellow fruit color. Sunlight intensity was observed to affect fruit color. The upper portions of red fruits were more intensely colored than the side which was away from the sun. Yellow fruits also tended to show a faint pink blush on the side exposed to direct sunlight. When yellow fruits were covered with black bags, this tendency disappeared. The age of the fruit was also observed to affect color development. Some yellow fruits which had become over-ripe on the trees developed some red streaks. Finally, red fruits which were diseased showed the distribution of color in patches of red and yellow, the lesions becoming yellow while unaffected areas of the fruits remained red.

Orange versus Red Ripe Fruit Color: An attempt was also made to study the inheritance of orange ripe fruit color. Unfortunately no fruit set was obtained in the cross between C. monoica which produced orange

colored fruits and the C. goudotiana female plant used in the study of inheritance of red and yellow ripe fruit colors. However, another red-fruited C. goudotiana plant set fruits with C. monoica when the latter was used as the source of pollen. The progenies of this cross were used in determining the mode of inheritance of orange and red ripe fruit colors.

Mortality rate was high among F_2 plants and only 52 plants reached the fruiting stage. It was possible to make only one backcross (to the orange-fruited parent) because the original C. goudotiana female plant was lost before F_1 plants had begun to flower. The results of this cross are presented in Table XXIII.

TABLE XXIII

Segregation of red and orange ripe fruit colors in a cross between red-fruited and orange-fruited species of Carica

Cross/generation	Fruit color segregation			Observed ratio			Chi-square
	# Red	# Pink	# Orange	Red	Pink	Orange	
Red x Orange ....(F_1)	0	21	0	0	1	0	
Pink selfed ....(F_2)	11	28	13	1	2	1	0.46
Pink x Orange ....(BC)	0	35	41	0	1	1	0.47

Ripe fruit skin color of F_1 hybrids was neither red nor orange but pink. This was suggestive of lack of dominance between the alleles responsible for the production of orange and red fruits. A ratio of 1 red : 2 pink : 1 orange was observed in the F_2. Backcrossing F_1 plants to the orange parent produced orange and pink fruits in an approximate ratio of 1 pink : 1 orange. From the limited data available it seems both orange and red ripe fruit colors are under the control of two alleles with no dominance. The various studies done with the peppers, Deshpande (1933), Smith (1950), El Hassan and Smith (1970) showed that red ripe fruit color was dominant to yellow. These traits were shown to be under the control of a single pair of genes. However, results obtained by these same authors indicated that red fruit color was completely dominant to orange. Mode of inheritance was also monogenic. Variations in intensity of distribution of red color were observed but the connection between these and light intensity was not mentioned.

Branching: Two forms of branching were observed among the species studied. One form was typical of C. cauliflora and the other was typified by C. monoica. C. cauliflora branched late during vegetative growth and as a result, had a very distinct main trunk. Branches arose only from the lower half of the plant and at a considerable distance from ground level. Branches were few, usually only about two to four branches per tree. This type of branching is referred to here as 'sparse branching'. (Figs. 26 and 27). Fig. 27 shows a basal branch.

C. monoica on the other hand, branched very early during vegetative growth and the main trunk was barely distinct. The branches arose very close to the ground level and there were several to many branches per plant. This type of branching is referred to here as 'bush branching'. (Fig. 28). All F_1 hybrids were branched profusely close to ground level like C. monoica. Of a total of 95 F_2 plants, 68 exhibited bush branching and 27 were sparsely branched. These results were not significantly different from a ratio of 3 bush : 1 sparse. The chi-square value of 0.59 with a probability between 0.500 and 0.250 was obtained. A total of 85 plants were scored in the backcross (to C. cauliflora) progeny. Of these, 40 were profusely branched and 45 were sparsely branched. A chi-square value of 0.29 with a probability between 0.750 and 0.500 showed that this segregation fitted a 1 : 1 ratio. A backcross to C. monoica produced only profusely branched plants.

These results are suggestive of a difference of a single pair of genes between these two forms of branching with bush branching dominant to sparse branching. Perhaps the basic reason for the differences observed in the mode of branching lies in the degree of apical dominance possessed by these two species. Three plants of C. cauliflora that were accidentally decapitated by a storm sprouted several lateral branches. It is very likely that C. cauliflora has a strong apical dominance which can suppress the growth of lateral branches. C. monoica on the other hand, has a weak apical dominance which allows the profuse production of secondary branches. It would be interesting to compare auxin production and auxin destruction capabilities of both species.

PLATE VII: Showing the types of branching exhibited by *C. cauliflora*, *C. monoica* and their hybrid.

Figures:

26. *C. cauliflora* (unbranched)
27. *C. cauliflora* (only a single branch)
28. *C. monoica* (profusely branched)
29. *C. cauliflora* x *C. monoica* (profusely branched)


26


27


28


29

Inheritance of Fruit Configurations: One of the morphological characters studied was fruit configurations. Each fruit had five distinct longitudinal lines running from the stem end of the fruit to the blossom end. The ovary wall was made up of five fused carpels. Since it was the ovary wall which formed the rim of the fruit, these lines probably represented the points of fusion of the five carpels. Three types of fruit configurations were observed among the species reported here. In C. goudotiana and C. parviflora these lines occurred as narrow ridges giving the fruits a markedly pentagonal appearance in cross section. In C. cauliflora and C. pennata the lines occurred in the form of narrow grooves. In C. monoica and Index No. 203 the lines also occurred as grooves which were wider and shallower than those of C. cauliflora and C. pennata, giving the fruits a nearly smooth surface (Figure 30).

A cross between C. parviflora and C. goudotiana (both with ridged fruits) yielded F_1 plants producing only ridged fruits. The F_1 female plants of a cross between C. cauliflora and C. pennata (both with narrow grooves) produced only fruits with narrow grooves. Similarly, F_1 plants of a cross between Index No. 203 and C. monoica (both with wide grooves) produced fruits with only wide grooves. These results indicated that all the three types of fruit configurations bred true.

Two successful crosses were used in the study of inheritance of fruit configurations. A cross between C. cauliflora (narrow grooves) and C. monoica (wide grooves) yielded 45 F_1 plants all of which produced only fruits with wide grooves like those of C. monoica. Out of a total of 96 F_2 plants 75 produced fruits with wide grooves like

those of C. monoica and 21 produced fruits with narrow grooves similar to those of C. cauliflora. A chi-square value of 0.50 indicated that the segregation fitted a 3 : 1 ratio. Backcross of the F_1 plants to C. cauliflora (narrow grooves) produced 50 fruiting plants. Out of these, 23 produced fruits with wide grooves and 27 produced fruits with narrow grooves. This segregation was not significantly different from a 1 : 1 ratio. The chi-square value was 0.32.

All the F_1 hybrids of the cross C. goudotiana (ridges) x C. monoica (wide grooves) produced fruits with ridges. From a total of 51 F_2 plants reaching the fruiting stage, 37 produced ridged fruits and 14 produced fruits with wide grooves. A chi-square value of 0.16 was suggestive of a 3 : 1 ratio. Backcross to C. monoica yielded 73 fruiting plants, 35 of which produced ridged fruits and 38 produced grooved fruits. This fitted a 1 : 1 ratio. The chi-square was 0.12.

No cross involving narrow grooves and ridges could be made because of cross incompatibility. The results of inheritance of fruit configurations are presented in Tables XXIV and XXV.

TABLE XXIV

Segregation of ridged and widely grooved fruits in a cross between C. goudotiana (ridged) and C. monoica (widely grooved)

Cross/generation	Fruit configuration segregation		Ratio observed		Chi-square
	# ridged	# wide grooves	ridges	wide grooves	
Ridged x wide grooves...(F_1)	21	0	1	0	
F_1 ridged selfed .....(F_2)	37	14	3	1	0.16
F_1 ridged x C. goudotiana (BC_1)	52	0	1	0	0.00
F_1 ridged x C. monoica (BC_2)	35	38	1	1	0.12

TABLE XXV

Segregation of narrow and wide grooved fruits in a cross between C. cauliflora (narrow grooves) and C. monoica (wide grooves)

Cross/generation	Fruit configuration segregation		Ratio observed		Chi-square
	# wide grooves	# narrow grooves	wide grooves	narrow grooves	
Narrow grooves x wide grooves...F_1	45	0	1	0	
F_1 wide grooves selfed.....F_2	75	21	3	1	0.50
F_1 wide grooves x C. cauliflora..BC_1	23	27	1	1	0.32
F_1 wide grooves x C. monoica.....BC_2	39	0	1	0	0.00

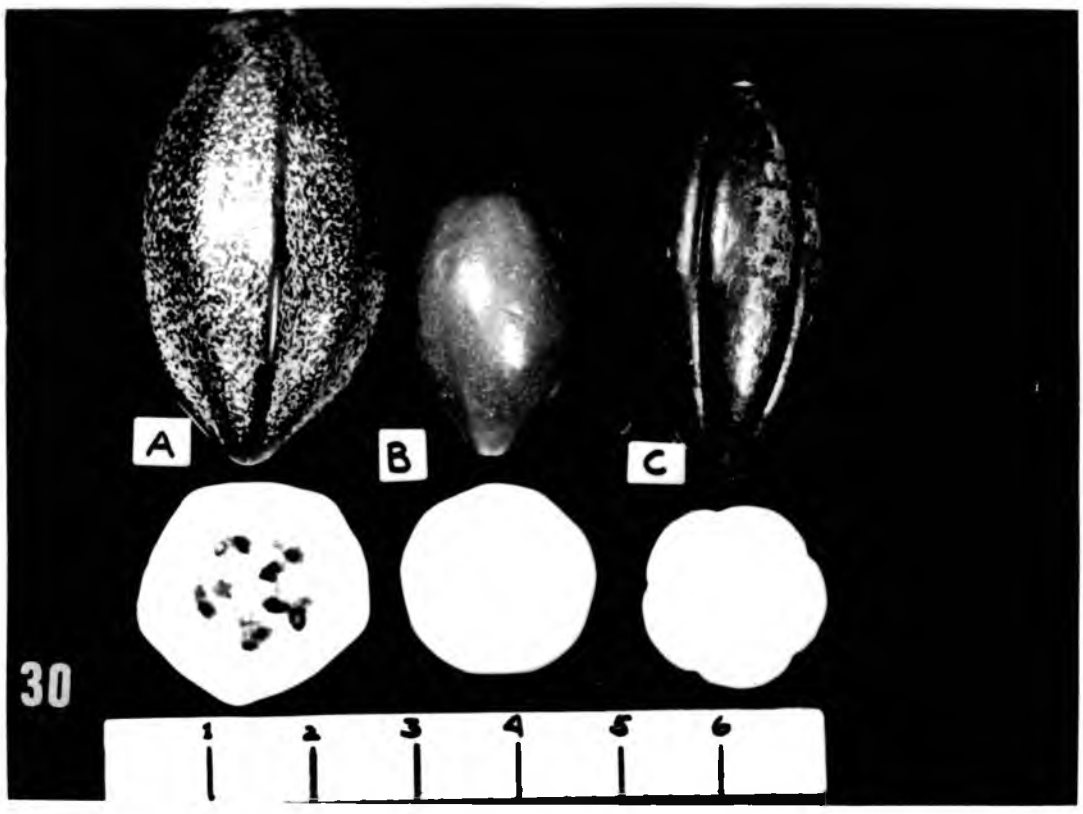
PLATE VIII: Some fruit and seed coat characteristics of C. goudotiana, C. monoica and C. cauliflora. (Scale in inches)

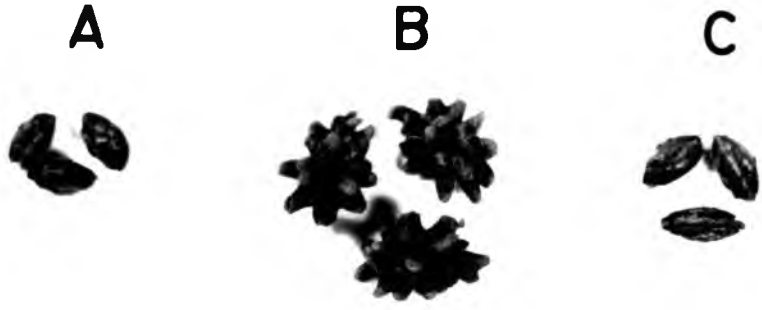
Figures:

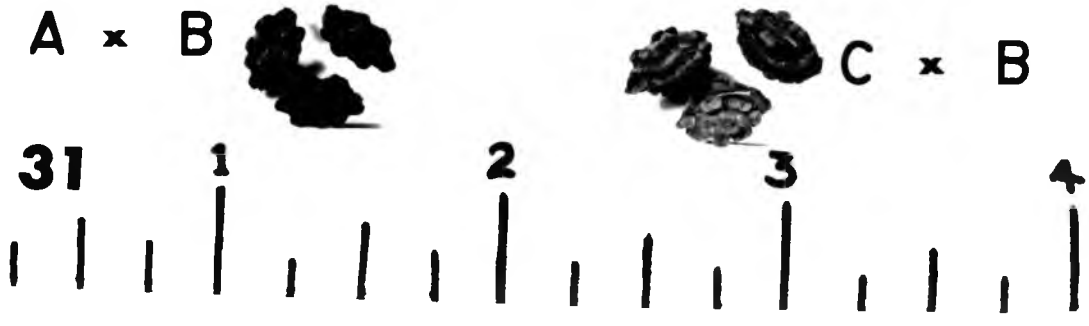
30. Fruit ridges of C. goudotiana (A), note the somewhat pentagonal appearance of cross section; Fruit grooves of C. monoica (B), showing the wider and flatter nature of grooves; Fruit grooves of C. cauliflora (C), showing the narrow and deeper appearance of grooves.

31. Appearance of seed coat of C. goudotiana (A), C. monoica (B) and C. cauliflora (C). Note the spiny nature of the seed of C. monoica versus the relatively smooth ones of C. goudotiana and C. cauliflora. The seed coat spines of the hybrids (A x B) and (C x B) tend to be intermediate between those of the parents.

VIII







Inheritance of Succulent Pulp: In all the species studied here except C. monoica, seeds were produced in the fruit cavity which was filled with a succulent soft pulp. In C. monoica this pulp was dry and cottony in texture. The results of two crosses between C. monoica and two other species which produced a succulent pulp are presented in Table XXVI.

TABLE XXVI

Segregation of succulent and dry fruit pulp in crosses between three species of Carica

Cross	F_1 pulp	F_2		BP_1		BP_2	
		Succulent	Dry	Succulent	Dry	Succulent	Dry
C. cauliflora P_1 x C. monoica P_2	All succulent	61	25	52	0	18	20
C. goudotiana P_1 x C. monoica P_2	All succulent	35	17	40	0	30	38
	Total	96	42	92	0	48	58

All classification was done when fruits were fully ripe. All the F_1 hybrids produced fruits with a succulent pulp.

The cross C. cauliflora x C. monoica yielded 86 F_2 plants in a proportion of 61 succulent to 25 dry. Backcross to C. cauliflora (succulent) yielded 52 plants all of which produced fruits with a succulent pulp. Only 38 plants reached maturity in the backcross of the F_1 hybrid to C. monoica (dry). Out of these, 18 produced succulent fruits and 20 produced dry fruits. A similar segregation pattern was

also observed in the cross C. goudotiana x C. monoica. Out of a total of 52 F_2 plants, 35 produced succulent fruits and 17 produced dry fruits. Backcross to C. goudotiana yielded 40 females all of which produced succulent fruits. A total of 68 plants was raised from the backcross of the F_1 plants to the dry parent. Out of these, 30 produced succulent fruits and 38 produced dry fruits.

Since both crosses produced similar results the data were pooled for analysis (Table XXVII).

TABLE XXVII

Chi-squares of succulent and dry pulp in F_2 and backcross progenies of crosses between three Carica species

Generation	Observed		Expected		Chi-square
	Succulent	Dry	Succulent	Dry	
F_2	96	42	103.5	34.5	2.17
BP_1	92	0	92	0	0.00
BP_2	48	58	53	53	0.94

F_2 segregation ratio approximated 3 succulent pulp : 1 dry pulp. Backcrosses to the dry parent produced both succulent and dry pulps in an approximate ratio of 1 : 1.

These results indicated a monogenic mode of inheritance for succulent and dry pulps with complete dominance for succulent pulp and recessiveness for dry pulp.

Inheritance of Seed Coat "Spines": Two types of seed coat morphology were observed among the species under investigation. When the fruit of C. monoica is very young the coat of the immature seed is nearly smooth. However, as the fruit develops the seed coat becomes progressively spiny. At full maturity the seed is covered with numerous spines. These spines were described by Warmke et al. (1954) as prominent horn-like projections. For ease of comparison these horn-like projections characteristic of the seed coat of C. monoica are hereby called seed coat spines. In all the other species studied, the immature seed coat in the very young fruits is nearly smooth but as the fruits develop the seed coat becomes spiny. However, at ripening of the fruit the spines disappear leaving behind little scars. These scars were described by Warmke et al. (1954) as low irregular protuberances. To facilitate classification, this category of seed coat is hereby referred to as non-spiny. On account of the different developmental stages traversed by the seed coat, all classification was done when fruits were fully ripe.

Crosses were made between C. monoica (spiny) and C. cauliflora (non-spiny) and between C. monoica (spiny) and C. goudotiana (non-spiny). The results of these crosses with respect to seed coat character in the F_1, F_2 and backcross progenies are presented in Table XXVIII.

All F_1 hybrids of both crosses produced seeds with projections intermediate in size between those of the two parents. These were simply classified as intermediate. In the F_2 populations three types of seed coat morphology were observed. In addition to the intermediate

types like those produced by the F_1 plants, there were those which were as spiny as those of C. monoica and others which were non-spiny. The three types were produced approximately in a ratio of 1 spiny : 2 intermediate : 1 non-spiny. Backcross to the spiny parent produced both intermediate and spiny types in an approximate ratio of 1 intermediate : 1 spiny. Backcross to C. cauliflora (non-spiny) produced intermediate and non-spiny types also in a ratio of 1 : 1. The data were pooled and subjected to a chi-square test. The analysis is presented in Table XXIX.

TABLE XXVIII

Segregation of spiny and non-spiny seed coats in progenies of crosses between C. cauliflora, C. goudotiana and C. monoica

Cross	F_1 seed coat	F_2 seed coat			BP_1 seed coat		BP_2 seed coat	
		spiny	intermediate	non-spiny	intermediate	non-spiny	spiny	intermediate
C. cauliflora P_1 x C. monoica P_2	intermediate	19	54	23	22	28	22	17
C. goudotiana P_1 x C. monoica P_2	intermediate	10	27	14	19	23	37	29
	Total	29	81	37	41	51	59	46

TABLE XXIX

Chi-squares of F_2 and backcross progenies of crosses between species producing spiny and non-spiny seed coats

Generation	Observed			Expected			Chi-square
	spiny	inter-mediate	non-spiny	spiny	inter-mediate	non-spiny	
F_2	29	81	37	36.75	73.50	36.75	2.40
BP_1	0	41	51	0	46	46	1.09
BP_2	59	46	0	52.5	52.5	0	1.61

A ratio of 1 : 2 : 1 in the F_2 generation and a ratio of 1 : 1 in backcross progeny were indicative of a simple mode of inheritance of this character with dominance lacking. These results confirmed those which Warmke et al. (1954) observed in a cross between C. goudotiana and C. monoica. Figure 31 shows the types of seed spines mentioned above.

Sex Inheritance: The species investigated here were all dioecious except C. monoica and C. papaya. Results of sib-matings and crosses among dioecious species are presented in Table XXX. A total of 289 F_1 plants was raised from these crosses and sib-matings. Out of these, 143 were male plants and 146 were female. A chi-square value of 0.003 indicated that this ratio was not significantly different from a 1 : 1 ratio as expected.

TABLE XXX

Sex segregation in crosses and sib-matings among some species of Carica

Cross/sib-mating		# Male	# Female
Female	Male		
C. goudotiana (red)	x C. goudotiana (red)	49	45
C. goudotiana (red)	x C. goudotiana (yellow)	39	34
C. parviflora	x C. parviflora	12	10
C. cauliflora	x C. cauliflora	33	31
C. cauliflora	x C. pennata	9	11
Index No. 203	x C. cauliflora	11	15
	Total	143	146

No fruit set was obtained in crosses between C. papaya and any of the other species studied here. C. monoica is strictly monoecious and very stable with regard to its sex, (Horovitz, 1967). In the present study three generations of selfing C. monoica produced only monoecious plants with pistillate and staminate flowers. Five crosses were made between dioecious species and C. monoica, using the latter as the source of pollen. The dioecious species involved in these crosses included two variants of C. goudotiana (149R and 195), two variants of C. cauliflora (145 and 194) and Index No. 203. Results of these crosses are presented in Table XXXI.

TABLE XXXI

F_1 sex form of crosses between Carica monoica and plants of some dioecious species

Cross	F_1 sex form		
	# monoecious	# male	# female
C. cauliflora (145) x C. monoica	24	0	0
C. cauliflora (194) x C. monoica	27	0	0
C. goudotiana (149R) x C. monoica	18	0	0
C. goudotiana (195) x C. monoica	10	0	0
Index No. 203 x C. monoica	26	0	0
Total	105	0	0

Owing to poor germinability of F_1 seed only a total of 105 hybrid plants were established from these crosses. All F_1 plants were monoecious. All the F_1 hybrids of the cross C. cauliflora (145) x C. monoica, in addition to producing strictly pistillate and staminate flowers, also produced quite often some carpellodic flowers in which both stamens and pistil occurred together. The number of stamens in all the carpellodic flowers examined was five. The stamens had a tendency to be partially fused to the wall of the mis-shapened ovary of the pistil. These flowers set carpellodic fruits. Sawant (1958) also reported the appearance of carpellodic flowers in the cross C. monoica x C. cauliflora. The occurrence of carpellodic flowers and fruits, a phenomenon frequently encountered in C. papaya, was not observed in any of the other species under investigation here. Carpellodic flowers were also observed in all

the F_1 hybrids of the other crosses but their occurrence was very rare and carpellodic fruits were hardly ever set.

In the F_1 hybrids of the cross C. goudotiana (149R) x C. monoica, the production of staminate (male) flowers was nearly completely suppressed. Female flowers were produced with preponderance all year round. The production of male flowers tended to be periodical and only very few male flowers were produced relative to the number of female flowers produced. Production of male flowers coincided with the summer months.

This tendency for suppression of production of male flowers was not observed in the F_1 hybrids of the other variant of C. goudotiana, (195) and C. monoica. These results are in general agreement with those obtained by Warmke et al. (1954) and Horovitz and Jimenez (1967). Warmke et al. found that a cross between C. goudotiana and C. monoica (source of pollen) produced all monoecious F_1 plants. These authors used the yellow fruited form of C. goudotiana which was probably the same as Index No. 195 used here. Horovitz and Jimenez (1967) confirmed Warmke's results. In addition, Horovitz and Jimenez reported that a cross between C. cauliflora and C. monoica, using the latter as the pollen parent, produced only monoecious F_1 hybrids. However, neither sex reversal nor suppression of production of male flowers was mentioned by these authors in connection with the F_1 hybrids.

F_2 generations were raised from three out of the five crosses made between dioecious species and monoecious C. monoica. F_2 plants segregated into monoecious and female types. No males were observed. The sex segregation patterns observed among the F_2 plants are shown in

Table XXXII.

TABLE XXXII

Results of sex segregation among F_2 plants in three crosses involving dioecious and monoecious *Carica* species

Cross	Sex segregation F_2		Approximate ratio observed		Chi-square
	# monoecious	# female	monoecious	female	
C. cauliflora (145) x C. monoica	77	19	3	1	1.39
Index No. 203 x C. monoica	60	25	3	1	0.88
C. goudotiana (149R) x C. monoica	33	19	3	1	3.69

The F_2 plants of all three crosses segregated in an approximate ratio of 3 monoecious : 1 female. All the monoecious F_2 plants of the cross, *C. cauliflora* (145) x *C. monoica* also produced carpellodic flowers and fruits like their F_1 parents. Flowers and fruits of the F_2 plants of the cross between Index No. 203 and *C. monoica* were normal.

Production of male flowers in the F_2 generation of the cross, *C. goudotiana* (149R) x *C. monoica* was also partially suppressed in most of the monoecious plants. Out of the 33 monoecious plants observed in the F_2 generation of this cross, 12 produced flowers of both sexes

regularly and no suppression of male flowers was detected. The remaining 21 showed partial suppression of production of male flowers. The ratio of presence of partial suppression to lack of it was approximately 2 : 1. Horovitz and Jimenez (1967) also obtained a ratio of 3 monoecious to 1 female in F_2 generations of crosses involving female plants of C. cauliflora, C. goudotiana and C. monoica (as pollen parent).

No backcross was made to Index No. 203 because the female plant (the only one planted here) was lost. Earlier work by Horovitz and Jimenez (1967) had shown that backcrosses of the F_1 hybrids to female plants of C. cauliflora and C. goudotiana yielded progenies which segregated in a ratio of 1 monoecious : 1 female. In the present studies F_1 plants were used as female parents and crossed with pollen from C. monoica, C. goudotiana (149R) and C. cauliflora. Results of these backcrosses are presented in Table XXXIII.

TABLE XXXIII

Sex ratios observed in backcrosses of F_1 monoecious hybrids to C. monoica, C. cauliflora and C. goudotiana using the three species as pollen parents

Cross	Sex segregation			Approximate ratio observed			Chi-square
	# monoecious	# female	# male	monoecious	female	male	
(C. cauliflora x C. monoica) F_1 x C. monoica	39	0	0	1	0	0	
(C. cauliflora x C. monoica) F_1 x C. cauliflora	20	30	48	1	1	2	2.00
(C. goudotiana x C. monoica) F_1 x C. monoica	66	0	0	1	0	0	0.00
(C. goudotiana x C. monoica) F_1 x C. goudotiana	-	52	59	-	1	1	0.44
(Carica species 203 x C. monoica) F_1 x C. monoica	42	0	0	1	0	0	0.00

When pollen from C. monoica (monoecious) was used to pollinate the pistillate flowers of the monoecious F_1 plants only monoecious plants were produced. However, when pollen from the male plants of the dioecious species C. cauliflora and C. goudotiana was used to pollinate the female flowers of the F_1 hybrids, entirely different results were obtained. For C. cauliflora, such a "backcross" resulted in the production of plants which segregated in an approximate ratio of 2 male : 1 female : 1 monoecious. When pollen from male C. goudotiana (149R) was used to pollinate female flowers of the F_1 hybrids a ratio of 1 male : 1 female was obtained. Monoecious types were completely absent. The reason for the complete absence of monoecious plants in this cross was not apparent and further work is definitely needed to throw light on this.

Attempt was made to study sex segregation in reciprocal crosses. A reciprocal cross between C. monoica (monoecious) and C. cauliflora, using the latter as the male parent, yielded 39 F_1 hybrid plants. Unlike the original cross which produced only monoecious F_1 plants, the reciprocal produced 16 males and 23 monoecious. This approximated a ratio of 1 monoecious : 1 male (chi-square value was 1.26) and confirmed Sawant's results (1958). No one had succeeded previously in obtaining fruit set between C. monoica and C. goudotiana using the latter as source of pollen, Warmke (1954). In the present studies, however, after many repeated attempts a total of eight fruits was set. These had not ripened three months after the cross was made.

Horovitz and Jimenez (1967) proposed a hypothesis for sex determination in some Carica species including C. cauliflora, C. goudotiana

and C. monoica. The following genotypes were suggested for the different sex forms: XX (female), XY_1 (male) and XY_2 (andromonoecious), the combinations Y_1Y_1, Y_1Y_2, and Y_2Y_2 being lethal. C. monoica, a strictly monoecious species and constant with regard to its sex form was assumed to be homogametic with the genotype ZZ. The Z chromosome presumably contains F genes for the development of the gynaecium and an Am gene for the development of the androecium. This hypothesis further assumed that the X chromosomes of C. cauliflora and C. goudotiana carry the recessive allele am so that in crosses involving these two species and C. monoica (pollen parent) the combination ZX is monoecious.

The results of the crosses studied here in which pollen from C. monoica (ZZ) was used in pollinating the female plants of the dioecious species, C. cauliflora (XX), C. goudotiana (XX) and Index No. 203 (XX) were in keeping with the expectations of this hypothesis. All the F_1 hybrids were monoecious confirming that the combination XZ is monoecious. It must be mentioned however that the partial suppression of the development of the androecium observed in the F_1 hybrid of C. goudotiana (red) and C. monoica, was not expected on the basis of the hypothesis. It would seem that the "X" chromosome of C. goudotiana female had some factor/s which possessed a tendency to suppress at least partially the development of the androecium.

A ratio of 3 monoecious : 1 female obtained in the F_2 plants was also in agreement with the stipulations of the hypothesis. F_1 genotype was XZ. Therefore, the F_2 genotypes with regard to sex would be as follows:

1 ZZ	:	2 XZ	:	1 XX
(monoecious)		(monoecious)		(female)

This would give 3 monoecious : 1 female as observed in the F_2 plants. Here again a partial tendency to suppress the production of male flowers was observed in the F_2 plants which resulted from the C. goudotiana (red) and C. monoica cross. Approximately 2/3 of the monoecious plants showed this tendency. This phenotypic ratio of 2 (partial suppression) : 1 (lack of suppression) corresponded to the genotypic ratio of 2 XZ : 1 ZZ indicating that the "X" chromosome of C. goudotiana (red) in combination with Z results in partial suppression of the development of the androecium.

When the female flowers of the F_1 hybrids of both crosses were pollinated with the pollen from C. cauliflora and C. goudotiana male plants, two entirely different sets of results were obtained. In the case of C. cauliflora this cross produced plants which segregated in a ratio of 2 male : 1 female : 1 monoecious. This would be expected if the combination YZ gave a male plant as follows:

F_1 hybrid (XZ) x C. cauliflora, male (XY)

Result:	XX	XZ	YX	YZ
	female	monoecious	male	male

This would be a ratio of 2 male : 1 female : 1 monoecious.

In case of C. goudotiana this cross yielded 1 male : 1 female. Monoecious types were completely absent. A ratio of 1 male : 1 female in the cross (XZ x XY) could only be obtained if (a) the combinations XZ and YZ were lethal, or (b) the combination XZ gave a female. Results obtained in the F_1 hybrids cancelled the first possibility. Considering the second possibility, it may be recalled that the combination XZ in case of C. goudotiana (red) x C. monoica did cause a

suppression of androecium development in all the F_1 plants and in 50% of the F_2 plants. However, the suppression was partial and periodically a few male flowers were produced. It would seem that the X chromosome of the female plant of C. goudotiana (red) only partially suppressed the development of the androecium while the X chromosome of the male plant completely suppressed androecium development. The reason for this is not apparent and would require further investigation. Cases of complete suppression of androecium development by the X chromosomes of female plants of dioecious species have been reported by Horovitz and Jimenez (1967). These species include C. pubescens, C. stipulata, C. microcarpa and C. horovitziana. A cross between C. monoica and the female plant of any of these species would produce only female F_1 plants indicating that the combination XZ here produced a female rather than monoecious. Horovitz and Jimenez (1967) explained this by assuming that the X chromosomes of C. pubescens, C. microcarpa, C. stipulata and C. horovitziana carry an Su^{Am} gene which is a dominant suppressor of Am and hence of development of the androecium. Differences in degree of suppression of androecium development by the X chromosomes of the different sexes of the same species were not mentioned.

The reciprocal cross between C. monoica and C. cauliflora using the latter as a male parent produced F_1 hybrids in a ratio of 1 monoecious : 1 male. This was according to expectation if the X chromosome of the male plant of C. cauliflora did not suppress the formation of androecium and the combination YZ produced a male plant.

C. monoica (ZZ)	x	C. cauliflora, male (XY)	
F_1	1 XZ (monoecious)	:	1 YZ (male)

If the X chromosome of the male plant of C. goudotiana possesses a factor for the complete suppression of androecium development then a reciprocal cross between C. monoica and C. goudotiana using the latter as the source of pollen should produce F_1 plants which segregate in a ratio of 1 male : 1 female instead of 1 male : 1 monoecious. As mentioned above eight fruits have set in this cross but not yet ripe. If viable seed is obtained it will be useful to score for sex segregation among the progeny. This could elucidate some of the unexpected results obtained in the original cross.

From these results it would seem that the monoecious and dioecious conditions in the species studied were determined by the pollen parent. If the pollen from a monoecious species was used in pollinating the female flower of a dioecious species, all F_1 plants would be monoecious. However, if the pollen from a dioecious species was used to pollinate the female flower of a monoecious species the F_1 plants would segregate in a ratio of 1 monoecious : 1 male such as obtained in the case of C. cauliflora. This mechanism conforms to the Ecballium type (cf. Westergaard, 1958) and confirms results obtained previously by Horovitz and Jimenez (1967) in the cross between C. cauliflora and C. monoica (pollen source). The case of C. goudotiana (red) showing partial suppression of the development of the androecium by the female plant and its complete suppression by the male plant was unique and calls for furhter investigation. These results do indicate that the male and female plants of the same species differ with respect to their sex determination mechanism.

From the data available it is highly probable the genotype XX is

female and XY is male. If C. monoica is ZZ as proposed by Horovitz and Jimenez (1967) then the hybrid combination YZ is also male while XZ is either monoecious or female depending on the dioecious species involved in the cross.

Cytology and Cytogenetics: Studies of microsporogenesis were conducted on seven plants including four species and three interspecific hybrids. The parental species investigated were C. parviflora, C. monoica, C. cauliflora and C. goudotiana (red). The interspecific hybrids studied included C. parviflora x C. goudotiana, C. cauliflora x C. monoica and C. goudotiana (red) x C. monoica.

All species and hybrids were found to possess nine pairs of chromosomes. Pairing of chromosomes was mostly normal. However, pairing between the homologues of a certain pair sometimes seemed to be only partial. It is also possible that terminalization of chiasmata produced this effect. Occasionally lack of any pairing at all was also detected between these sister chromosomes. Figures 53 - 58. This feature was observed in diakinasis and metaphase I and occurred frequently in C. cauliflora, C. goudotiana, C. cauliflora x C. monoica and C. goudotiana x C. monoica. It must be emphasized that lack of complete pairing between two members of one pair was not detectable in all the dividing cells.

Precocious separation of one chromosome pair at anaphase I was observed in all the species and the interspecific hybrids. This separation and movement of one chromosome pair ahead of all the other eight pairs sometimes occurred early in metaphase I. It was observed

that partial pairing and precocious anaphasic separation involved the same pair of chromosomes. In cases where synapsis was found to be incomplete, a difference in size between the two supposed homologues could be detected. Smallness of chromosomes coupled with their high condensation made detailed study of the morphology of the disjoining homologues difficult. However, in the hybrid C. goudotiana x C. monoica, certain dividing cells were observed in which there were eight complete bivalents and two univalents. The two univalents lay side by side with no physical contact. These cells provided a good opportunity to study the morphology of these two homologues. It was found that there was an apparent difference in size. The smaller chromosome had its centromere at the center (metacentric). The bigger one had its centromere nearer one end showing the presence of a long arm and a short arm. Size difference between the two homologues was also observed in the hybrids, C. cauliflora x C. monoica and C. parviflora x C. goudotiana in which both homologues were also found disjoined at diakinasis. In the species, C. cauliflora, complete lack of pairing between these homologues was also observed in certain cells at metaphase I. Size difference between the two sister chromosomes was unquestionably obvious. An apparent difference in size between the two homologues was also observed in certain cells of C. goudotiana and C. parviflora after they had undergone precocious separation.

Precocious separation of a pair of chromosomes at anaphase I had been observed in the male and hermaphrodite trees of C. papaya, Kumar et al. (1945), Storey (1953). The occurrence of this phenomenon has been suggested as an evidence of the presence of sex chromosomes in

C. papaya. However, morphological differences between the disjoining sister chromosomes could not be detected. As reported above differences in morphology were found between the sister chromosomes in C. cauliflora, C. goudotiana, C. parviflora, C. goudotiana x C. monoica, C. cauliflora x C. monoica and C. parviflora x C. goudotiana. It would seem that difference in size led to partial pairing (partial homology) which in turn set the stage for precocious separation at anaphase I. The presence of a heteromorphic pair which undergoes partial synapsis and precocious anaphasic separation strongly indicates the existence of sex chromosomes in the species and hybrids mentioned above. Two of the three hybrids were monoecious plants and the third was dioecious. The three species were dioecious. It must be mentioned that in C. monoica (monoecious) no size difference was detectable between the sex chromosomes although partial pairing and precocious separation did occur.

Chromosome lagging at anaphase was sometimes observed in two of the hybrids examined. The hybrids which showed this feature were C. parviflora x C. goudotiana and C. cauliflora x C. monoica. The lagging could involve one, two and sometimes three chromosomes. Such lagging was not found in the parent species studied. This might be an indication that certain gametes might carry less than the gametic number of chromosomes, in this case, nine. If this occurred and such gametes were functional, the production of aneuploids could ensue.

Regularity of bivalent formation found in the interspecific hybrids was expected considering the high degree of fertility exhibited by all the hybrids. No hybrids produced showed sterility. Similar observations were reported by Zerpa D.M. (1959) in her cytological investigation

of six interspecific hybrids of the genus, Carica. This would seem to indicate high genetic affinity between the parental species involved in the crosses.

Except for the heteromorphism found between the members of the sex pair, no detectable chromosomal differences, suggestive of differences in the source of genetic variation were observed. It is most likely that the morphological differences observed among the species investigated simply reflect differences in gene products modified by environmental influences, (cf. Stebbins, 1971).

PLATE IX: Chromosomes of four Carica species and three interspecific hybrids as seen in diakinasis. Meiotic observations were made on the pollen mother cells (P.M.C.). Magnification : x 2,700.

Figures:

32. C. cauliflora 145 (dioecious).

33. C. monoica (monoecious): arrow points at partially paired chromosomes.

34. C. cauliflora 145 x C. monoica (monoecious): arrow points at partially paired chromosomes.

35. C. goudotiana 149R x C. monoica (monoecious): arrows point at members of the suspected sex pair.

36. C. parviflora (dioecious).

37. C. parviflora x C. goudotiana (dioecious): arrows point at two unpaired sister chromosomes. Note size difference between the two homologues.

38. C. goudotiana 149R (dioecious): arrow points at partially paired chromosomes.

IX

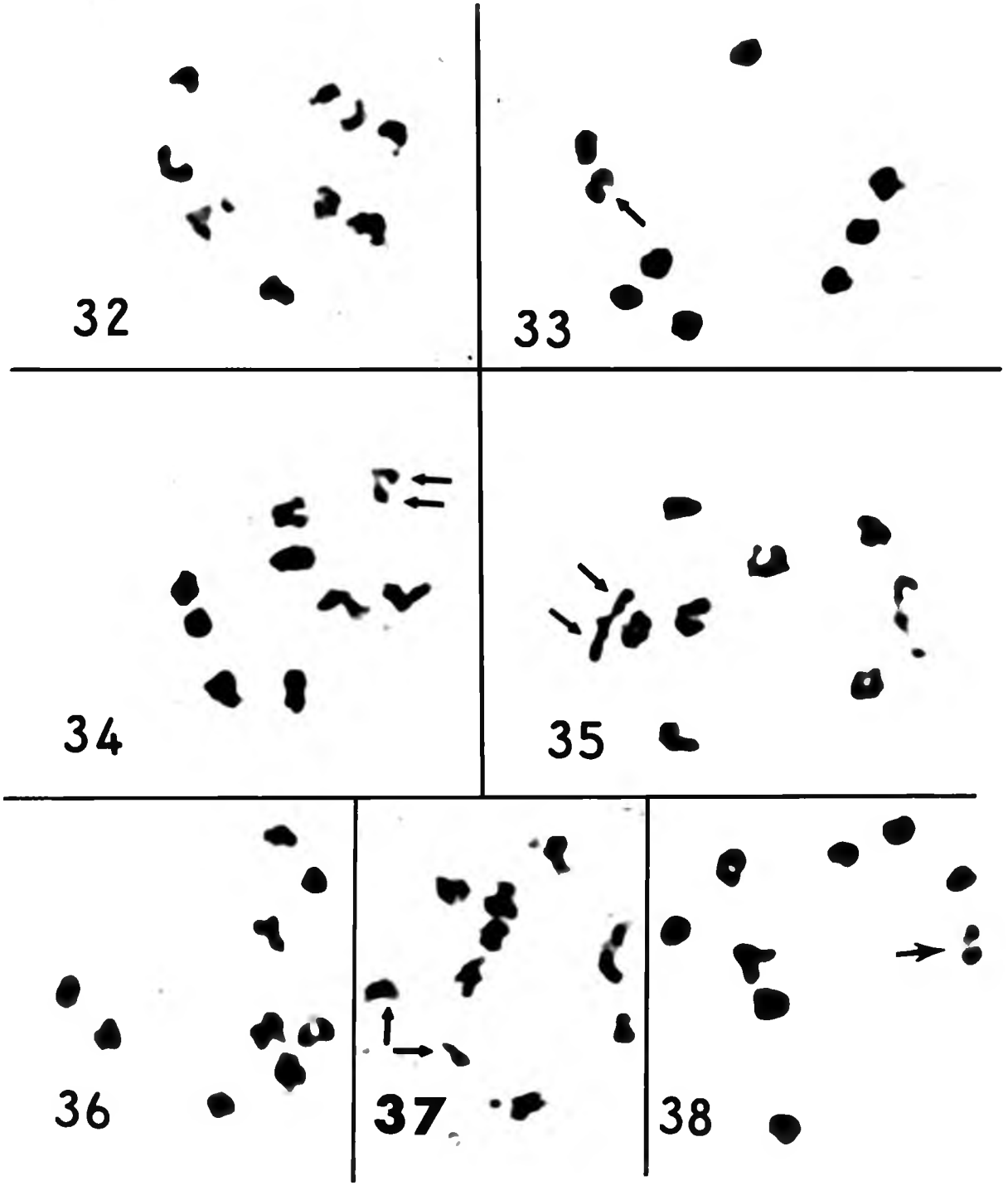


PLATE X: Chromosomes of four Carica species and three inter-specific hybrids as seen in metaphase I. Meiotic observations were made on the pollen mother cells (P.M.C.). Magnification : x 2,700.

Figures:

39. C. cauliflora 145 (dioecious). Note partial pairing as indicated by arrow.

40. C. monoica (monoecious). Note partial pairing as indicated by arrow.

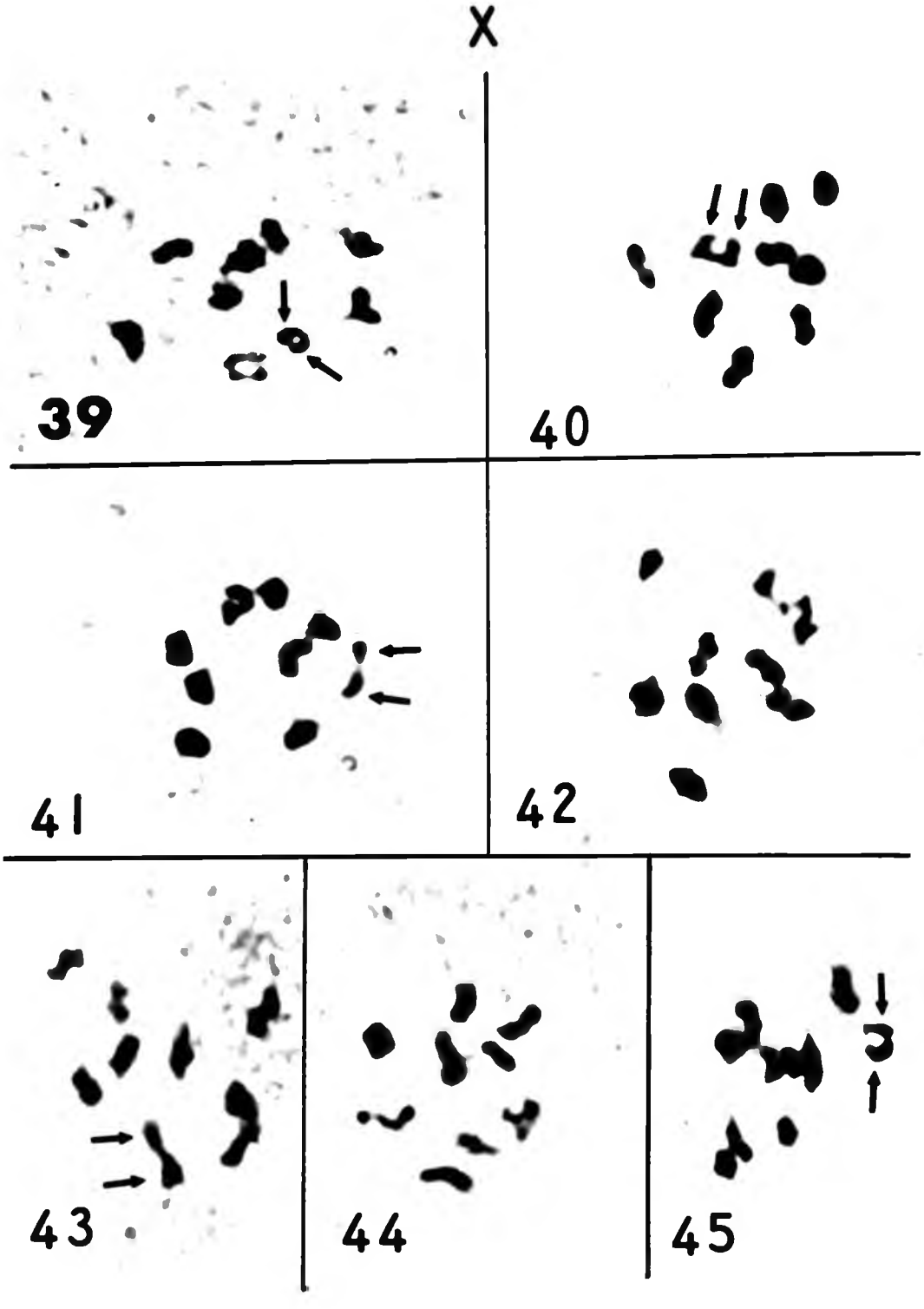
41. C. cauliflora 145 x C. monoica (monoecious). Note partial pairing as indicated by arrow.

42. C. goudotiana 149R x C. monoica (monoecious). Note partial pairing as indicated by arrow.

43. C. parviflora (dioecious). Note partial pairing as indicated by arrow.

44. C. parviflora x C. goudotiana 149R (dioecious).

45. C. goudotiana 149R (dioecious). Note partial pairing as indicated by arrow. (chiasma terminalization?)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45

PLATE XI: Metaphase I plates of four Carica species and three interspecific hybrids showing precocious anaphasic separation of the homologues (arrows) of one pair of chromosomes. Note slight differences in size of disjoined sister chromosomes (arrows). Magnification : x 2,700.

Figures:

46. C. cauliflora 145 (dioecious). Note difference in size of disjoined chromosomes (the one to the left slightly bigger than the one to the right).
47. C. monoica (monoecious). Size difference not obvious.
48. C. cauliflora 145 x C. monoica (monoecious).
49. C. goudotiana 149R x C. monoica (monoecious).
50. C. parviflora (dioecious). Note size difference between separated homologues, the upper one bigger than the bottom one.
51. C. parviflora x C. goudotiana (dioecious).
52. C. goudotiana 149R (dioecious). Size difference noticeable (the homologue at the bottom appears bigger than the one on top).

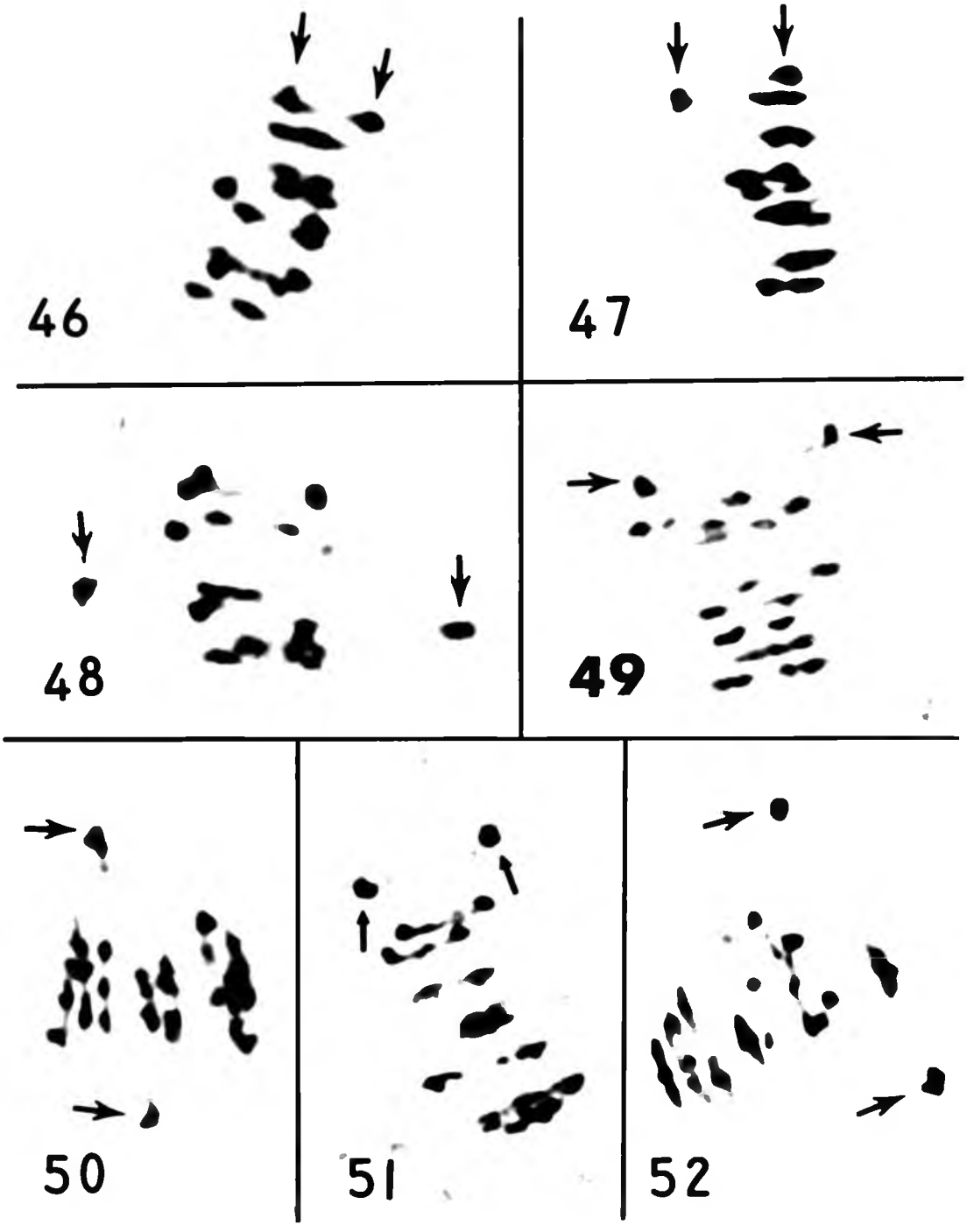
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PLATE XII: Chromosomes of four Carica species and two interspecific hybrids at various meiotic phases to show partial synapsis, lack of pairing and slight size differences sometimes observed between the sister chromosomes of the suspected sex pair (indicated by arrows).
Magnification : x 2,700.

Figures:

53. C. cauliflora 145 (dioecious). Arrows point at unpaired members of the 'sex' pair. Note the obvious size difference between the two homologues.

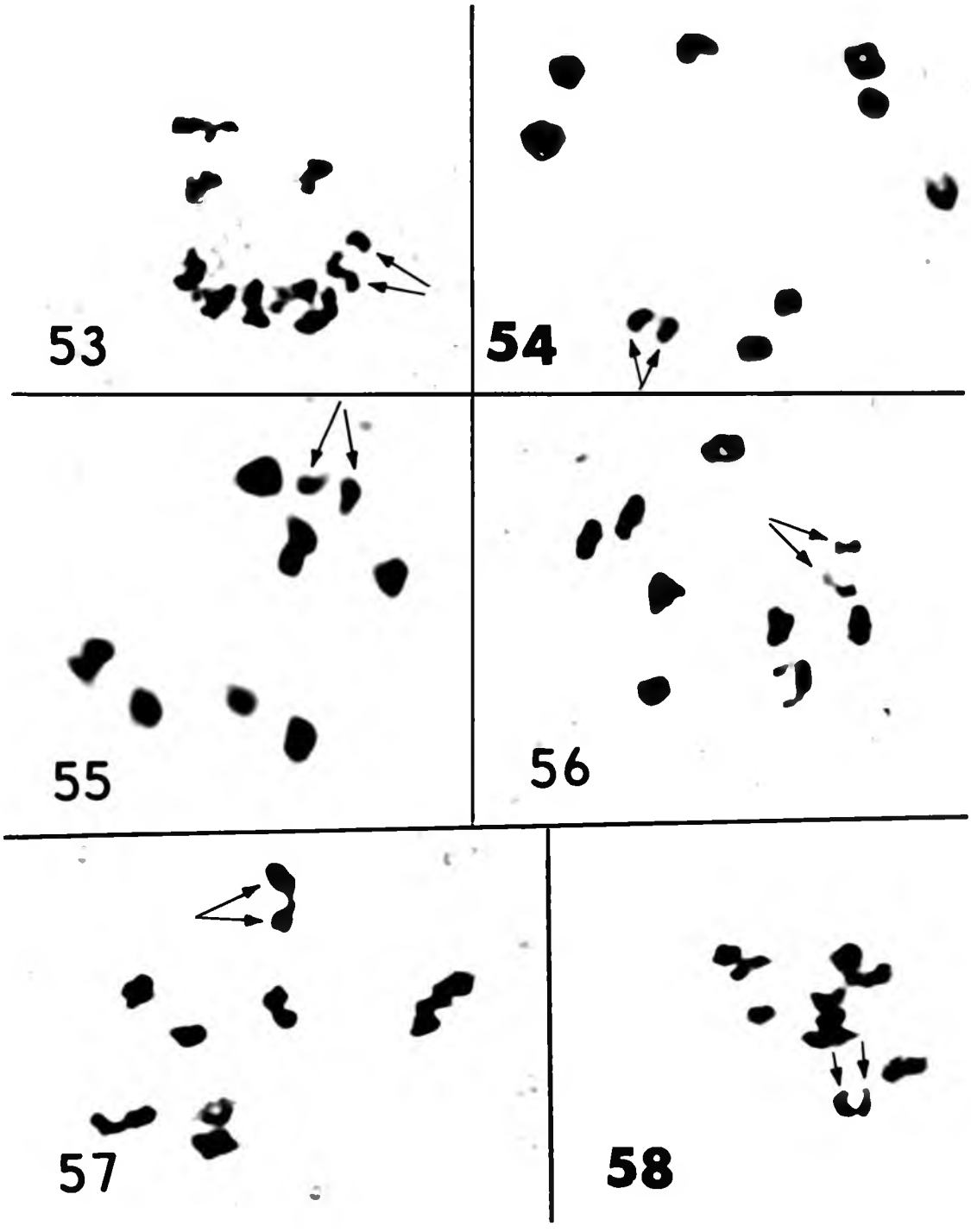
54. C. monoica (monoecious). Arrows point at loosely associated members of the sex pair. No size difference is noticeable.

55. C. cauliflora 145 x C. monoica (monoecious). Arrows point at the unpaired sister chromosomes of the sex pair. Note size difference between the homologues.

56. C. goudotiana 149R x C. monoica (monoecious). Arrows indicate members of sex pair. Note differences in size and morphology of homologues.

57. C. parviflora (dioecious). Arrows show partially paired members of the sex pair. Note size difference between sister chromosomes.

58. C. goudotiana (dioecious). Arrows point at sister chromosomes of the sex pair, here paired only at their terminals (chiasma terminalization?) Slight difference in size noticeable.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58

PLATE XIII: Showing normal movement of chromosomes at anaphse I and an occasional tendency of some chromosomes of certain hybrids to lag at anaphase. Arrows indicate chromosomes tending to lag. Magnification : x 2,700.

Figures:

59. C. cauliflora 145 (normal)

60. C. monoica (normal)

61. C. cauliflora x C. monoica (normal)

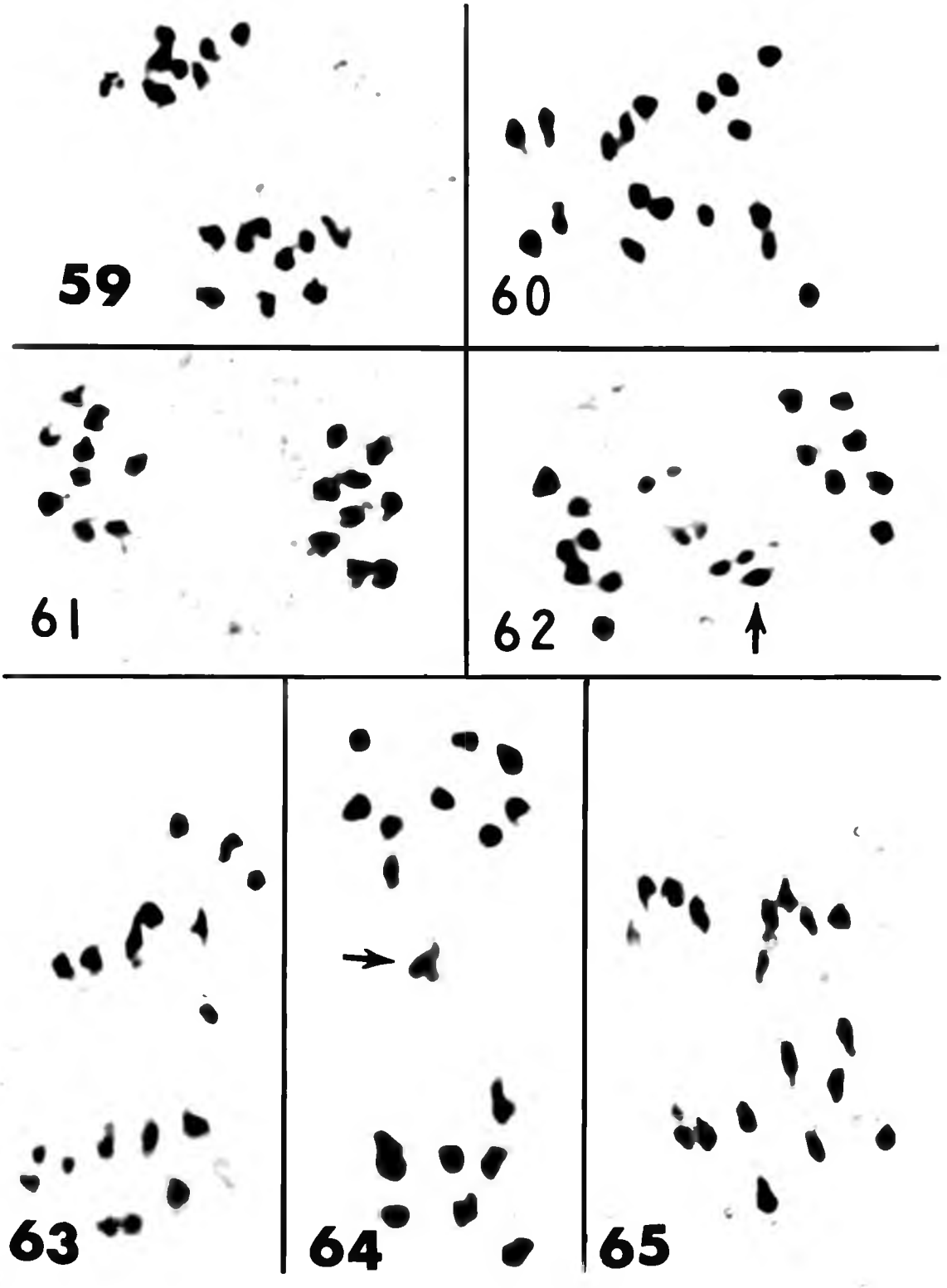
62. C. cauliflora x C. monoica (tendency to lag)

63. C. parviflora x C. goudotiana (normal)

64. C. parviflora x C. goudotiana (tendency to lag)

65. C. parviflora (normal)

XIII



SUMMARY AND CONCLUSION

These experiments were undertaken to study: (1) floral biology, (2) cross-compatibility, (3) heterosis, (4) cytogenetics and (5) inheritance of certain distinct characteristics among nine Carica species and their hybrids. The characteristics investigated included stem color, petiole color, flower color, fruit color, branching, fruit configurations, fruit pulp, seed spines and sex.

Studies of floral anthesis showed that all species except C. parviflora had peak anthesis between early evening and late at night. C. parviflora reached maximum anthesis between 8 and 10 a.m. Results of floral anthesis of three interspecific hybrids are also presented. Time of maximum anthesis of hybrids tended to approximate that of one of their parents suggesting genetic control of floral anthesis. Anther dehiscence occurred as early as 48 hours prior to floral anthesis. Results also indicated a genetic control of time duration between floral bud appearance and floral anthesis.

Results of pollen germination in vitro showed that all species produced viable pollen. There were marked differences in percentage germination of pollen at different pH levels. Generally, lower pH (4.5 - 7.5) was more favorable to pollen germination than higher pH (8.5 - 9.5). Significant differences were also found between different species in terms of pollen germination. Pollen of C. papaya and C. goudotiana showed lower germination percentages than pollen of other species. Results also indicated interaction between pH and species. Pollen of C. cauliflora and C. monoica showed wider adaptability to

range in pH than that of the other species studied.

Studies of self and sib-pollinations showed that all species were self compatible to various degrees. Viable seed was set in all cases. Cross compatibility studies showed crosses that were fertile and yielded viable seed, crosses which set fruit but produced empty seeds, crosses that set parthenocarpic fruits and crosses which failed to set fruit. Two crosses, C. parviflora x C. goudotiana and C. monoica x C. goudotiana (male), which had not been successfully made (Warmke, 1954, Horovitz and Jimenez, 1967), were successful after several attempts. A diagrammatic scheme of cross-compatibility found between species is presented. Fertile crosses were not obtained between C. papaya and any of the other species, indicating a rather distant relationship between C. papaya and other species studied in this work.

A total of 10 hybrids including nine interspecific and one intra-specific hybrids were made. A general description of these plants is presented. Hybrid vigor (heterosis) was established in two of the crosses studied. Comparisons were made between F_1 hybrids and their high parents. Heterosis was shown in terms of eight-month tree height, eight-month trunk circumference, total number of fruits set and total weight of fruits produced. Observations on inbreeding depression were inconclusive because of confounding with the "replant problem". Results of inheritance studies are summarized in Table XXXIV.

TABLE XXXIV

Summary of the mode of inheritance of the characters investigated

Character	Mode of inheritance
1. Stem color (red versus green)	Monogenic: red dominant to green; modifier genes indicated.
2. Petiole color (red versus green)	Monogenic: red dominant to green; modifier genes indicated.
3. Flower color:	
(a) purple-blush versus pale yellow	Monogenic: purple-blush dominant to pale yellow.
(b) white versus pale yellow	Monogenic: white dominant to pale yellow.
(c) purple-blush versus pink	? : pink dominant to purple-blush.
4. Fruit skin color:	
(a) red versus yellow	Monogenic: red dominant to yellow.
(b) red versus orange	Monogenic: no dominance.
5. Branching (bush versus sparse)	Monogenic: bush dominant to sparse.
6. Fruit configurations:	
(a) ridges versus wide grooves	Monogenic: ridges dominant to wide grooves.
(b) wide grooves versus narrow grooves	Monogenic: wide grooves dominant to narrow grooves.
7. Fruit pulp (succulent versus dry)	Monogenic: succulent dominant to dry pulp.
8. Seed coat morphology (spiny versus non-spiny)	Monogenic: no dominance.

Sex inheritance studies revealed differences in sex determination mechanism between male and female plants of the same species. Crosses between dioecious species and monoecious species using the latter as pollen source produced only monoecious F_1 plants. F_2 generations of three of these crosses produced a ratio of 3 monoecious : 1 female. Backcrossing F_1 plants to C. cauliflora (male) produced a ratio of 2 males : 1 female : 1 monoecious. However, backcrossing the F_1 to C. goudotiana (149R, male) produced only males and females in a ratio of 1 male : 1 female. This indicates that sex determination mechanism in C. cauliflora (male) differs from that in C. goudotiana (149R, male). The reciprocal cross using pollen from C. cauliflora on the stigma of pistillate flower of monoecious C. monoica yielded F_1 plants in a ratio of 1 male : 1 monoecious.

Differences in degree of suppression of the androecium were indicated in crosses involving both male and female plants of C. goudotiana (149R) and C. monoica. The female exhibited partial suppression of androecium while the male showed complete suppression of androecium. Further studies are needed to clarify this finding.

The hypothesis for sex determination mechanism proposed by Horovitz and Jimenez (1967) was supported by results obtained in this study. The following genotypes with respect to sex suggested by Horovitz and Jimenez were confirmed: XY_1 (male), XX (female) and ZZ (monoecious C. monoica). The hybrid combination ZY was shown to be male and XZ could be monoecious or female depending on the dioecious species.

Cytological studies confirmed that both species and hybrids had 9 pairs of chromosomes. Partial pairing and subsequent precocious anaphasic separation involving one pair of homologues were observed in all species and hybrids investigated. Heteromorphism between these two homologues was detected in three species and three hybrids. These findings seem to justify the proposition that sex chromosomes do exist in these species and their hybrids.

Chromosome lagging at anaphase I was observed in two of the hybrids. This feature could result in the production of gametes with less than 9 chromosomes. Viability of such gametes might open the way to the formation of aneuploids.

The high fertility of hybrids was attributed to regularity of bivalent formation suggestive of close genetic affinity between parent species involved in crosses. Morphological differences between species were suggested to be most probably due to differences in gene products modified by environment rather than alterations in detectable chromosomal segments.

Speculations into the potentials of the wild Carica species

The wild species of the genus Carica have several potentials. They are relatively unexplored and form a sizeable pool of genetic material for basic studies such as those undertaken here. Such studies could produce valuable information on the fundamental knowledge of species relationships. Further studies on sex inheritance together with cytological investigation could throw additional light on the

problem of sex determination mechanism in Carica. Unlike C. papaya many of the wild species have colorful stems, leaf petioles, flowers and fruits which give them a potential ornamental value. There is a possibility that more species hybrids can be produced. The fact that two of the crosses hitherto described as impossible were successfully made justifies this possibility. The hybrid C. parviflora x C. goudotiana is a new plant with a considerable ornamental value. Color traits have been utilized as marker genes in several other plant genera.

All Carica species contain latex which might offer possibilities in the production of papaine, an important enzyme used in tenderizing meat. The nutritional value of some of these species is recognized in certain countries. It has been claimed, Swingle (1947), Warmke et al. (1954) that the cooked fruits and leaves of C. monoica are highly prized as items of food in Peru. C. goudotiana and C. pubescens are reportedly even of higher food value than C. monoica (Hamilton, personal communication). Because of the abundance of their production, there is the possibility that the fruits of some of these species could be made into animal food.

One of the objectives of this work was to find out how the information obtained from these studies could be utilized to improve C. papaya as a commercial crop. The question of gene incorporation into C. papaya from these species is problematical. There is the cross-incompatibility barrier which is rather a formidable one to overcome. It seems impossible to obtain fruit set with viable seeds in crosses between C. papaya and the other species of the genus. In the present

work crosses between male plants of C. cauliflora and C. goudotiana and hermaphrodite C. papaya produced undersize fruits which set a few empty seeds. Some of the immature seeds were filled with contents which however, had disappeared by the time seeds reached maturity. Even if the immature seeds could be grown by tissue culture, it would be difficult to say whether the resultant hybrids would be of any commercial value. Similar crosses to the female plants of C. papaya set parthenocarpic fruits.

It seems that papaya flavor is highly sensitive to genetic influence. In a study not reported in this manuscript there was a papaya mutant (Index No. 142) similar to C. papaya except that it produced very small rounded non-edible fruits. It was highly cross compatible with C. papaya. Crosses made between Index No. 142 and a papaya line, $26F_4$, a strain of high quality, produced fruits of good size but the fruit flavor was intolerable, and the flesh was soft, stringy and pungent smelling. It would be difficult to predict the number of backcross generations and selection necessary to improve the quality of this papaya fruit without losing other desirable traits. A result like this suggests that the possibility of improving C. papaya as a commercial crop by gene transfer from its wild relatives is very remote.

LITERATURE CITED

Agnew, G. W. J. 1941. Notes on pawpaw and its improvement in Queensland. Queensland Agr. Jour. 56:358-373.

Allard, R. W. 1966. Principles of plant breeding. Third Edition. John Wiley and Sons, Inc. New York. London. Sydney. 485pp.

Allen, P. 1963. Pollen studies in Carica papaya L. II. Germination and storage of pollen. So. Afr. Jour. Agr. Sci. 6(4):613-623.

Angell, F. F. and W. H. Gabelman. 1970. Inheritance of purple petiole in carrot, Daucus carota var. sativa. HortScience 5(3):175.

Badillo, V. M. 1967. Esquema de las Caricaceae. Agronomia Tropical 17(4):245-271.

Balsabramanyam, V. R. 1959. Studies on blossom biology of guava. Indian Jour. Hort. 16:69-75.

Barnes, D. K. et al. 1960. Inheritance of seed and flower colors in flax. Agronomic Journal 52:456-459.

Brewbaker, J. L. 1962. Cyanidin-red white clover: a duplicate recessive mutant in Trifolium repens L. Journal of Heredity 53:163-167.

_____ and B. H. Kwack. 1963. The essential role of calcium ion in pollen germination and pollen tube growth. Amer. Jour. Bot. 50(9):859-865.

Culp, T. W. 1960. Inheritance of paper shell capsules, capsule number and plant color in sesame. Journal of Heredity 51:146-148.

Darlington, C. D. and E. K. J. Ammal. 1945. Chromosome atlas of cultivated plants. London. George Allen and Unwin Ltd. 397pp.

Dasarathy, T. B. 1951. The guava. Madras Agricultural Journal 38:520-527.

Davis, D. W. et al. 1958. Impatiens balsamina L. The inheritance of floral colors. Genetics 43:16-34.

Deshpande, R. B. 1933. Studies in Indian chillies. III. The inheritance of some characters in Capsicum annuum. Indian Jour. Agri. Sci. 3:219-300.

El Hassan, G. M. and P. G. Smith. 1970. The inheritance of mature fruit color in Capsicum pubescens. R. and P. HortScience 5(3):174.

Erickson, H. T. and F. A. A. Conto. 1963. Inheritance of four plant and floral characters in Okra (Hibiscus esculentus L.). Proc. Amer. Soc. Hort. Sci. 83:605-608.

Gupta, B. D. and M. S. Sarma. 1954. The genetics of Corchorus (jute) VI. Inheritance of a new pigmentation pattern in Corchorus capsularis. Journal of Genetics 52:374-382.

Hamilton, R. A. 1954. Quantitative study of growth and fruiting in inbred and crossbred progenies from two Solo papaya strains. Haw. Agri. Exp. Sta. Tect. Bull. No. 20. 38pp.

Higgins, J. E. 1916. Growing melons on trees. Journal of Heredity 7:208-220.

_____ and V. S. Holt. 1914. The papaya in Hawaii. Haw. Agr. Expt. Sta. Bull. 32. 44pp.

Hirano, R. T. and H. Y. Nakasone. 1969. Pollen germination and compatibility studies of some Psidium species. Jour. Amer. Soc. Hort. Sci. 94:287-289.

Hofmyer, J. D. J. 1938. Genetical studies of Carica papaya L. So. Afr. Dept. Agr. and For. Sci. Bul. 187. 64pp.

_____. 1941. Genetics of Carica papaya L. Chron. Bot. 6:245-247.

_____. 1953. Sex reversal as a means of solving breeding problems of Carica papaya L. So. Afr. Jour. Sci. 49:228-232.

Horovitz, S. and H. Jimenez. 1967. Cruzamientos Interespecificos e intergenericos en Caricaceas y sus implicaciones fitotecnicas. Agronomia Tropical 17(4):323-343.

Jimenez, H. 1954. Determinacion del sexo en Carica papaya L. estructure hipotetica de los cromosomas sexuales. Agronomia Tropical 3(4):229-249.

_____. 1957. Injertos entre especies de Carica. Agronomia Tropical 7(1):33-37.

_____ and S. Horovitz. 1958. Cruzabilidad entre especies de Carica. Agronomia Tropical 7(4):207-215.

Jones, H. A. and G. N. Davis. 1944. Inbreeding and heterosis and their relation to the development of new varieties of onions. U. S. Dept. Agr. Tech. Bull. 874:1-28.

Kamemoto, H. and W. B. Storey. 1955. Genetics of flower color in Asystasia gangetica, Linn. Pacific Science 9:62-68.

Kumar, L. S. S. et al. 1945. The cytology of Carica papaya L. Indian Jour. Agr. Sci. 15:242-253.

Kwack, B. H. 1964. On the role of calcium and other cations in pollen germination and growth. Bot. Mag. (Tokyo) 77:327-332.

_____. 1965. The effect of calcium on pollen germination. Proc. Amer. Soc. Hort. Sci. 86:818-823.

Lawrence, W. J. C. 1931. The genetics and cytology of Dahlia variabilis. Journal of Genetics 24:257-304.

Lindsay, R. H. 1930. The chromosomes of some dioecious angiosperms. Amer. Jour. Bot. 17:152-174.

McClintock, B. 1929. A method for making acetocarmine smears permanent. Stain Technology 4:53-57.

Mehlquist, G. A. L. 1939. Inheritance in the carnation, Dianthus caryophyllus. I. Inheritance of flower color. Amer. Soc. Hort. Sci. Proc. 37:1019-1021.

Muhammad, S. U. et al. 1969. Hybrid vigour in Ricinus communis L. (castor oil). The Mad. Agr. Jour. 56(5):244-257.

Nakasone, H. Y. and W. B. Storey. 1955. Studies on inheritance of fruiting height of Carica papaya L. Amer. Soc. Hort. Sci. Proc. 66:168-182.

Odland, M. L. 1960. Inheritance of flower color in Capsicum annum L. Proc. Amer. Soc. Hort. Sci. 76:475-481.

_____ and C. J. Noll. 1950. The utilization of cross-compatibility and self-incompatibility in the production of F_1 hybrid cabbage. Proc. Amer. Soc. Hort. Sci. 55:391-402.

Paris, C. D. and W. J. Haney. 1958. Genetic studies in Petunia. I. Nine genes for flower color. Proc. Amer. Soc. Hort. Sci. 72:462-472.

Park, Soon Jai, and P. P. Rotar. 1968. Genetic studies in Spanish clover, Desmodium sandwicense E. Mey. I. Inheritance of flower color, stem color, and leaflet markings. Crop Science 8: 467-470.

Parker, J. C. et al. 1970. Combining ability estimates in Arachis hypogaea L. I. F_1 seedling responses in a controlled environment. Crop Science 10:429-432.

Randhawa, G. S. and P. K. R. Nair. 1960. Studies on floral biology of plum grown under subtropical conditions. Indian Jour. Hort. 17:83-95.

_____ and V. K. Damodaran. 1961. Studies on floral biology and sex-ratio in mango (Mangifera indica L.) var Chausa, Dasheri and Krishanbhog. II. Indian Jour. Hort. 18(1):51-64.

Robinson, H. F. et al. 1956. Dominance versus overdominance in heterosis: evidence from crosses between open-pollinated varieties of maize. Amer. Nat. 90:127-131.

Rotar, P. P. and Kuan-Hon Chow. 1971. Morphological variation and interspecific hybridization among Desmodium intortum, Desmodium sandwicense, and Desmodium uncinatum. Haw. Agr. Expt. Sta. Tech. Bull. No. 82. 28pp.

Santhanam, V. 1952. A note on the behaviour of three inter-racial hybrids in Gossypium arboreum L. The Mad. Agr. Jour. 39(6): 383-386.

Sawant, A. C. 1957. Crossing relationships in the genus Carica. Evolution 12(2):263-266.

_____. 1958. A study of the interspecific hybrid, Carica monoica x C. cauliflora. Proc. Amer. Soc. Hort. Sci. 71:330-333.

Scott-moncrief, R. 1936. A biochemical survey of some Mendelian factors for flower colors. Journal of Genetics 32:117-170.

Seaton, H. L. and J. C. Kramer. 1939. The influence of climatological factors on anthesis and anther dehiscence in the cultivated cucurbits. A preliminary report. Proc. Amer. Soc. Hort. Sci. 36:627-631.

Sharma, H. C. and P. N. Bajpai. 1969. Studies on floral biology of papaya (C. papaya L.). Indian Jour. Sci. and Ind. 3(1):9-18.

Singh, R. N. 1950. Studies in the floral biology of Trichosanthes Linn. Indian Jour. Hort. 7(1):1-13.

_____. 1954. Studies in floral biology and subsequent development of fruits in the mango (Mangifera indica L.) var. Indian Jour. Hort. 11(3):69-88. "Dasheri" and "Langra".

Singh, S. N. 1959. Testing viability of papaya pollen in artificial medium. Hort. Adv. 3:111-114.

_____. 1960. Longevity of papaya pollen. Indian Jour. Hort. 17:238-242.

_____ and H. S. Dhuria. 1960. Studies on floral biology of sweet lime. Indian Jour. Hort. 17:9-29.

Smith, H. H. 1937. Inheritance of corolla color in the cross N. langsdorfii by N. sanderae. Genetics 22:247-360.

Smith, P. G. 1950. Inheritance of brown and green mature fruit color in peppers. Journal of Heredity 41:138-140.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical Methods. Sixth Edition. The Iowa State Univ. Press, Ames, Iowa. 593pp.

Stambaugh, S. U. 1960. Forty years of papaya development. Fla. State Hort. Soc. Proc. 73:311-314.

Stebbins, G. L. 1971. Chromosomal evolution in higher plants. Addison-Wesley Publishing Company, Reading, Massachusetts. Menlo Park, California. London. Don Mills, Ontario. 216pp.

Storey, W. B. 1938. Segregations of sex types in Solo papaya and their application to the selection of seed. Proc. Amer. Soc. Hort. Sci. 35:83-85.

_____. 1940. Genetics of sex determination in papaya. Haw. Agr. Expt. Sta. Ann. Rpt. 1940:52-53.

_____. 1941. The botany and sex relations of the papaya. Haw. Agr. Expt. Sta. Bul. 87:5-22.

_____. 1953. Genetics of the papaya. Journal of Heredity 44(2): 70-77.

_____ and H. Kamemoto. 1947. Papaya. Haw. Agr. Expt. Sta. Biennial Rept. 1944-46:82.

Suguira, T. 1927. Some observations on the meiosis of the pollen cells of Carica papaya, M. rubra, A. japonica, and B. vulgaris. Bot. Mag. (Tokyo) 41:219-224.

Swingle, C. F. 1947. The Peruvian cooking papaya, Carica monoica, a promising new fruit and vegetable for the United States Corn Belt. Proc. Amer. Soc. Hort. Sci. 49:137-138.

Traub, H. P. and C. T. O'Rork, Jr. 1936. Papaya pollen germination and storage. Proc. Amer. Soc. Hort. Sci. 34:18.

Traub, H. P. et al. 1942. Papaya production in the United States. U. S. Dept. Agr. Cir. 633. 36pp.

Tysdal, H. M. et al. 1942. Alfalfa breeding. Nebr. Agric. Exp. Sta. Res. Bull. 124:1-46.

Vandenberg, P. and D. F. Matzinger. 1970. Genetic diversity and heterosis in Nicotiana. III. Crosses among tobacco introductions and flue-cured varieties. Crop Science 10(4):437-440.

Warmke, H. E., E. Cabanillas, and H. J. Cruzado. 1954. A new interspecific hybrid in the genus, Carica. Proc. Amer. Soc. Hort. Sci. 64:284-288.

Westergaard, M. 1958. The mechanism of sex determination in dioecious flowering plants. Advances in Genetics 9:217-273.

Wilson, R. F. 1941. Horticultural color chart 1 (1938) and 2 (1941). 203pp.

Wolf, H. S. and S. J. Lynch. 1940. Papaya culture in Florida. Fla. Agr. Expt. Sta. Bul. 350. 35pp.

Wynner, J. C. et al. 1970. Combining ability estimates in Arachis hypogaea L. II. Field performance of F_1 hybrids. Crop Science 10:713-715.

Yamane, G. M. and H. Y. Nakasone. 1961. Pollination and fruit set studies of Acerola, Malpighia glabra L. in Hawaii. Proc. Amer. Soc. Hort. Sci. 78:141-148.

Zerpa, Dora M. 1959. Cytologia de hibridos interespecificos en Carica. Agronomia Tropical 8(4):135-144.